OU_162659

THE EVOLUTION OF THE NERVOUS SYSTEM

THE EVOLUTION OF THE NERVOUS SYSTEM IN INVERTEBRATES VERTEBRATES AND MAN

BY

C. U. ARIËNS KAPPERS

M. D., Amsterdam, D. Sc., Yale University

DEDICATED TO
ELIZABETH CAROLINE CROSBY

CONTENTS.

PREFACE

— — —

The purpose of this book is to give a general survey of the nervous system, making the reader acquainted with its chief evolutionary principles and most characteristic forms in a short text, elucidated by many illustrations. I am fully aware that, in limiting my text, I run the risk of omitting details that may interest the reader. For such details I refer to the larger text books and original articles quoted in the text.

The chapter on the anthropology of the brain is written in the hope that it may increase the interest in this much neglected field and stimulate to more researches.

I want to express my thanks to Dr. C. J. VAN DER HORST and Dr. P. J. VAN DER FEEN Jr. for their valuable assistence in the field of invertebrate neurology, to Dr. S. GINSBURG and Rev. Dr. W. THOMSON for helping me in reading the proofs, (if the latter have not succeeded as well as they deserved, the fault is mine), to Dr. E. VAN 'T HOOG for making the index, and to our scientific artist CHR. VLASSOPOULOS for his excellent drawings.

<div align="right">C. U. ARIËNS KAPPERS</div>

Amsterdam, September. 1929.

THE EVOLUTION OF THE NERVOUS SYSTEM.

INTRODUCTION.

Nervous functions as general protoplasmatic functions.

Functions dominate forms but, on the other hand, do the forms which thus arise facilitate the functions, and bring them to perfections unknown before morphological differentiations occurred. In other words, special tissues are the result of activities already carried on before the tissue differentiation.

And so, dealing with the origin of the nervous system, we may ask whether in animals in which nervous elements are not yet differentiated, such as Protozoa and Sponges, functions are found that are comparable to nervous functions, differing from them only in degree.

Now this certainly occurs, since the principal functions of the nervous system: *reception, conduction, correlation* and *elaboration of impulses* are general properties of protoplasm, and, consequently, are present also in non-nervous tissue. They occur to a fairly extensive degree even in muscle tissue, the formation of which precedes (phylogenetically and ontogenetically) that of nerve cells. Thus, reflexes running even over long distances are seen in animals without any nervous tissue.

The same has been observed (WINTREBERT) [1]) in the larvae of higher animals before the differentiation of nerves has started, and also, in somewhat older larvae, after experimental removal of the brain and spinal cord rudiment (SCHAPER) [2]).

Moreover, it is very likely that even such functions as memory,

---

[1]) WINTREBERT. Sur l'existence d'une irritabilité excito-motrice primitive indépendente des voies nerveuses chez les embryons ciliés des Batraciens Comt. rend. de la société de Biologie de Paris, Tome 57, 1904.

[2]) SCHAPER. Experimentelle Studien an Amphibienlarven. I. Archiv für Entwicklungsmechanik der Organismen. Bnd. VI, 1898 p. 151. See especially p. 181.

attention and association, generally considered as features of mental life only and, as such, looked upon by most people as being exclusively functions of the brain, are inherent in living protoplasm in general.

As for *memory*, HERING [1]), in Vienna, showed this to be probable (1870), and LAYCOCK [2]) and BUTLER [3]) did the same shortly after and independently of him (1875, 1880). It is wellknown that SEMON [4]) elaborated the same idea in his book on the "*Mneme*", as he called this principle of memory in organic processes of heredity. Also DENDY [5]) accepted this view point.

As far as *attention* or concentration is concerned, I have recently [6]) pointed out that this process, which is adaptation to one function, to the exclusion of others, is the mental countrepart of a same process as occurs in the differentiation of *specific* tissues and organs from non (or less) specific cells in ontogenetic development. Finally, conscious *association* is the mental form of organic correlation, expressed in the nervous system by the phenomena of neurobiotaxis and in the rest of the organism in the form of cell connections.

Thus nervous activities such as reception, conduction and correlation of stimuli, are special developements of general properties of organic tissue in which even processes functionally analogous to memory, attention and association are inherent.

In Protozoa, and even in Sponges, no indication of nervous differentiation is seen, unless one were inclined to consider as such the fibrillar arrangement of conducting protoplasm in some Infusoria in connection with the ciliary apparatus [7]).

---

[1]) HERING. Über das Gedächtnis als eine allgemeine Function der organisierten Materie, Wien 1870.

[2]) LAYCOCK. A chapter on some organic laws of personal and ancestral memory. Journal of mental science. Vol. 21, 1875.

[3]) BUTLER. Unconscious memory, 1880.

[4]) SEMON. Die Mneme als erhaltendes Prinzip in Wechsel des organischen Geschehens, Engelmann, Leizig 1911.

[5]) DENDY. Outlines of evolutionary biology, London, 1921.

[6]) The logetic character of growth. Journ. of Comp. Neur. Vol. XXXI, 1919, p. 58 and Actions psychiques dans le développement organique, Acta zoologica. Vol. 1920. The logical character of mental processes is, according to my opinion, only a special case of the logical character of organic evolution.

[7]) SHARP. Diplodinium ecaudatum with an account of its neuro-motor apparatus. University of California publications in Zoology. Vol. 13, 1914. VISSCHER. A neuromotor apparatus in the ciliate Dileptus gigas. Journ. of Morph. and Phys. 1927.

In Coelenterates first *nerve cells* appear which exclusively serve conduction of stimuli and thus bring this function to a higher perfection. So the rapidity of conduction, which in non nervous tissue rarely exceeds 0,1 c.m. per second [1]), in the simplest nerve cells may rise to 45 c.m., in neurones to 10000 c.m. per second. Anatomically this perfection is shown by the long offshoots of these cells, which may carry an impulse uninterrupted over a distance of sometimes 1 M.

Neurosensory cells and primitive ganglion cells.

In the following pages I shall use the term *nerve cell* in a general sense for the different forms of *nervous conductors,* thus excluding the so called "sense cells" which are highly differentiated percipient cells, having however no conducting offshoots of their own (see p. 56).

The different forms of nervous conductors are three: the neurosensory cell, which generally retains its place in an epithelial layer [2]), the primitive or asynaptic ganglion cell and the polarized or synaptic neurone, both of which are nearly always located under the epithelium, though derived from it.

The *neurosensory* cell is the oldest form. It is an epithelial cell, generally provided with one or more sense hairs protruding into the surrounding medium, and a much longer basal offshoot, the neurite.

The sense hairs generally have pointed terminations, but they may bear knobs at their free ends. Where the sense hair is inplanted in the cell, "basal bodies" may be found, derivatives of the centrosomes, which however may also remain intact in the outer half of the cellbody or may even occur in the

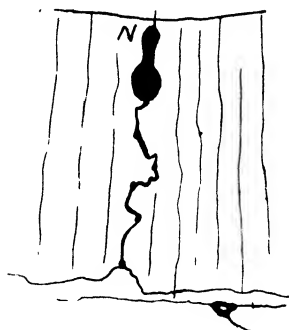Fig. 1. N.=Neurosensory cell in the epithelium of the enteroïd filament of Metridium dianthus (HAVET 1901). Underneath the epithelium a primitive ganglion cell.

[1]) BÜTTNER-WOBST. Ueber die Flimmerbewegung in Trachea und Bronchien, Dissertation, Jena, 1909. For Infusoria see *Taylor*, University of Caliiornia publications, Vol. 19, 1920.

[2]) Neurosensory cells may also lie under an epithelial layer.

knob of the sense hair itself (olfactory cells, VAN DER STRICHT [1]). While the sense hairs function in receiving the impulse, the neurite of the cell leading cellulo-fugally transmits the stimulus to other cells.

The neurosensory cell body and its neurite are provided with *neurofibrillae*. In other respects their structure is still very primitive, as no tigroid (or Nissl) substance, characteristic of ganglion cells and neurones, occurs in them, and as the neurite is never surrounded by a myeline sheath. It seems as if the lecithine which contributes to the formation of this sheath in real neurones, is still imbedded *inside* the neurite of the neurosensory cells. At least, AMBRONN [2]) and HELD could show the presence of this doubly refracting substance within the neurites of olfactory neurosensory cells.
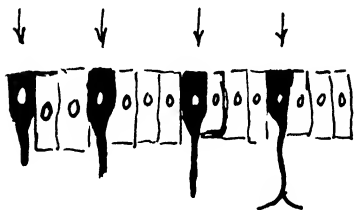

Fig. 2. Scheme of the development of neurosensory cells. The neurite grows away from the source of impulses in the same direction as the stimulation current (stimulocon-current).

The presence of the poorly conducting lecithine within the neurite may be responsible for its low conductivity, the rapidity of conduction being only 6—20 cm. [3]) per second according to NICOLAI, while in neurones provided with an external myeline sheath, it may rise till 100 M. per second, i.e. more than 500 times as fast.

An important fact concerned with neurosensory cells is that they always conduct in the same direction. Though experimentally the neurite is ambiconductive, yet physiologically, because of its position, it always transmits

---

[1]) V. D. STRICHT. Mémoires de l'Académie royale de medicine de Belgique, Tome 20, 1909. This and also the fact that the neurofibrillae may begin at the basal bodies (DAMMERMAN) suggests a special sensitiveness of centrosomes and their derivatives to external stimulations.

[2]) AMBRONN. Das optische Verhalten markthaltiger und markloser Nervenfasern. Bericht der math. phys. Klasse der Kön. Sachs. Gesellsch. der Wissensch. 1890. AMBRONN U. HELD. Die Entwicklung und Bedeutung des Nervenmarks, ibidem.

[3]) This has not been examined, as yet, in Invertebrates, where it may be still less. The rapidity of conduction here mentioned is that of the fila olfactiva of the pike. See NICOLAI. Ueber die Leitungsgeschwindigkeit im Riechnerven des Hechtes, Pflüger's Archiv. Bnd. 85, 1901.

away from the surface. *The neurosensory cell, consequently, is a polarized nerve cell*, resembling in this respect the real neurone more than it does the primitive ganglion cell.

Neurosensory cells differentiate from epithelial cells by the development of a neurite which grows away from the surface, following (and later leading) the stimulus in this direction. Its growth is *stimuloconcurrent* (fig. 2). It is interesting that even the body of the neurosensory cell has a slight tendency to follow the course of the impulses, which may explain why these cells are more numerous in the lower forms than in the higher, where they may give rise to the formation of subepithelial bipolar nerve cells (see p. 14).

Primitive ganglion cells are more highly differentiated than neurosensory cells, in so far as they are not only provided with *neurofibrillae*, but that their cell body contains tigroid substance (WOLFF), not occuring in neurosensory cells. In comparison, however, to
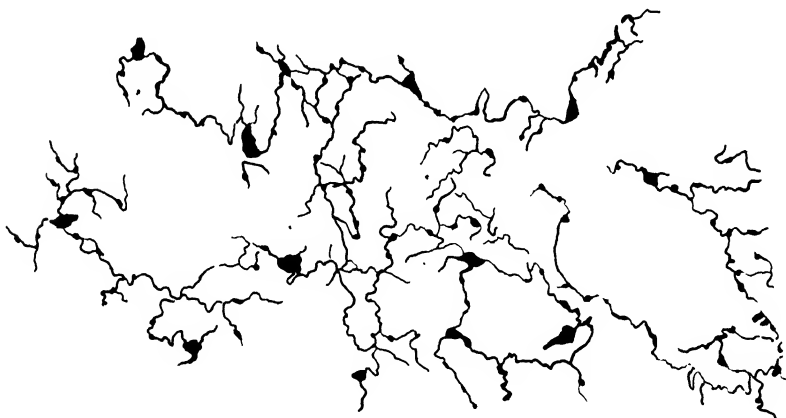
Fig. 3. Plexus [1]) of primitive ganglioncells and fibers in the tentacle of a Coelenterate, Heliactis bellis (WOLFF, 1903).

neurones, they are very primitive, as all their offshoots are identical showing no histological differentiation into dendrites and neurites while, physiologically, they conduct in both cellulo-fugal and cellulo-petal directions.

---

[1]) Wether the fibers of these plexuses are everywhere continnous, or if contiguity occurs is still doubtfull. See BOZLER Untersuchungen über das Nervensystem der Coelenteraten. Zeitschr. f. Wiss. Biol. Abt. II. Bnd 5, 1927.

Thus the nervous current in the umbrella of a Medusa may run clock wise, as well as in the opposite direction through the same plexus MAYER, c.f. p. 20). We call such a nervous network *asynaptic* (see fig. 3). Another primitive feature of these ganglion cells is that their offshoots are never provided with a myeline sheath. Accordingly their conductivity is slow. In Metridium (an anemone), PARKER [1]) found it to be 12—14 cm. (at 21° C.) per second, while HARVEY [2]) found that it is 46 cm. per second in a jellyfish. If we take the average of these figures (24 cm. per sec.) it is not much greater than the rate of conduction of neurosensory cells.

Such primitive ganglion cells are abundant in Coelenterates and Echinoderms, and are fairly numerous even in the basi-epitelial (subepidermal) plexus, of Vermes, Molluscs and Arthropods.

Two conceptions exist concerning their development.

The first has been advocated by KLEINENBERG (l. c. p. 16) who considered the so called neuro-muscular cells as their predecessors. These are epithelio-muscular cells, whose superficial part, though not specially differentiated, may carry a hair, while their basal processes are contractile (see fig 6). Although these epithelio-muscular cells certainly represent a very simple mechanism for reception, conduction and elaboration of stimuli, it is very doubtful if they are to be considered as the mother type of ganglion cells. Indeed, it has never been demonstrated that a ganglion cell arises from an epithelio-muscular cell, or from an embryonic cell similar to it.

SCHNEIDER [3]), studying the origin of the entodermal ganglion cell plexus in Coelenterates, found it to be derived from epithelial cells bearing no resemblance whatever to the so called neuro-muscular cells.

I feel more inclined to the opinion that these ganglion cells are derived from undifferentiated epithelium and so are more closely

---

[1]) G. H. PARKER. The rate of transmission in the nerve net of the coelenterates. Journ. of general physiology. Vol. 1, 1918.

[2]) HARVEY. Some recent experiments in the nature of nervous transmission. Journal of nervous and mental diseases. Vol. 45, 1922.

[3]) SCHNEIDER. Histologie von Hydra fusca mit besonderer Berücksichtigung des Nervensystems der Hydroidpolypen. Arch. f. microsc. Anat. Bnd. 35, 1890. Einige histologische Befunde an Coelenteraten. Jenaische Zeitschr. f. Natur-wissenschaft. Bnd. 27, 1902.

allied to neurosensory cells, as defended first by the HERTWIGS and later by ZOJA and DROOGLEEVER FORTUYN.

The conception that primitive ganglion cells may be allied to neurosensory cells is supported by an observation made by VON LENDENFELD [1]) in young specimens of Cyanea, where this author found ganglion cells still lying *in* the epithelial layer, resembling young neurosensory cells, while such cells could no more be observed in adult specimens where the ganglioncells were all located under the epithelium. An observation made by WOLFF, who found ganglioncells extending their fibers between the epithelium is also in favor of this conception.

The *polarized* ganglioncells or *neurones* are certainly closely related to the neurosensory cells.

The neurone and the synaps. Neurobiotaxis.

The *neurones*, which first appear in worms, in addition to neurosensory cells and primitive asynaptic ganglion cells, are characterized by the fact that they have two kinds of offshoots, which lead the impulses in different ways. Their receptory offshoots or *dendrites*, generally multiple (Fig. 4), lead the stimulus towards the cell (cellulo-petally), whereas the single [2]) neurite leads it away from the cell (cellulo-fugally). This, however, is not the consequence of a monoconductive character of each of these offshoots, since experiments show that the neurite, as well as the dendrites, may lead stimuli in either direction. If either of them be stimulated in the midst of its course, the nervous current runs in both directions from the point of stimulation (KÜHNE's experiment).

But physiologically such stimulations rarely occur, the mutual relations of neurones and their position in reference to receptors and

---

[1]) v. LENDENFELD. Ueber Coelenteraten der Südsee. Zeitschr. f. wissensch. Zool. Bnd. 37, 1882. Ueber das Nervensystem der Hydroidpolypen Zool. Anz. Bnd. 6, 1883.

[2]) For the explanation of this polydendritism and monoaxonism, and other details concerning the neurobiotactic differentiation of the neurone I refer to my papers in the Journal Comp. Neurology, 1917, and in Brain, 1921 and to my Vergleichende Anatomie des Nervensystems der Wirbeltiere (Bohn, Haarlem, 1920).
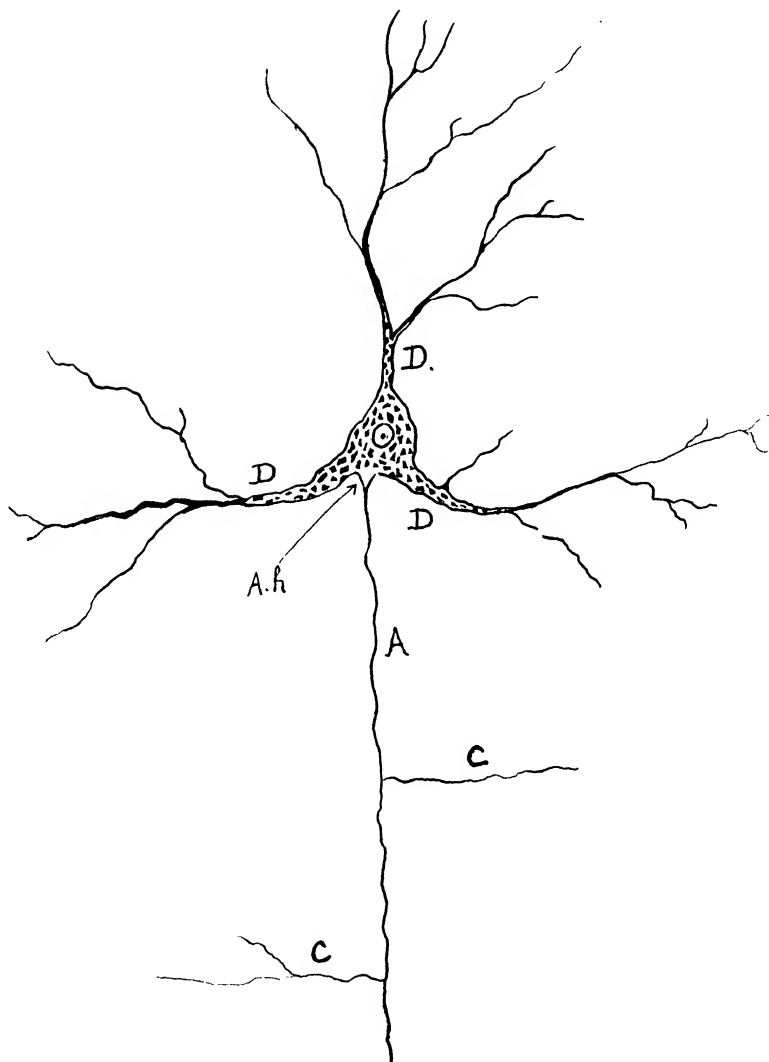
Fig. 4. Multipolar neurone of the cortex of a cat, with three large dendrites (D). The axon (A), arising from the axon hillock (A.h.) has two collaterals (C).

effectors causing their dendrites to be passed nearly always, cellulo-petally, the neurite cellulofugally [1]).

This, however, is true for the neurosensory cells as well, since these are so located that they can receive stimuli only with their cell-bodies, so that the neurite must always lead cellulo-fugally.

Consequently, polarization does not occur first in neurones.

The neurones differ, however, from neurosensory cells by the fact that they have developed large and usually many recipient dendrites, while in the latter the cell body itself or a short peripheral elongation of it is the only recipient.

The dendrites thus establish an increase of the recipient surface, compared to neurosensory cells. Besides, the cellbody as well as the dendrites of neurones contain *tigroid substance*, which is not seen in the body of the neurosensory cell.

This, however, at the same time proves that the dendrites retain the character of the cellbody, of which they are *non specific* parts. They even share its trophic, especially its anabolic functions, as also appears from the presence of *oxydases* in both, whereas the neurite and its *initial hillock* (fig. 4) has neither tigroid substance nor oxydases.

This is in agreement with the smaller rôle played by the neurite in metabolism, especially in anabolism in which the neurite may depend upon the perikaryon more than does the dendrite.

That the neurite however has also metabolic functions is shown by the fact that it secretes CO^2 even while at rest, and that this secretion increases about 15 % during action (c.f TASHIRO [2]) and PARKER [3])).

The *very specific* character of the neurite is also indicated by the fact that there is never [4]) more than one neurite, while there may be many dendrites of one cell.

The neurite probably contains more ionizable potassium salts than the dendrites do (MACALLUM, MACDONALD), and this may explain its

---

[1]) In the sympathetic system (comp. p. 89) even in true neurones, axon-reflexes occur, i. e. nervous stimuli may flow cellulo-petally in the neurite, spreading over its collaterals.

[2]) TASHIRO. A chemical sign of life. University of Chicago Press 1917. TASHIRO. Studies on alkaligenesis in tissues I Ammonia production in the nerve fiber during excitation. Amer. Journ. of Physiol. Vol. 60, 1922.

[3]) PARKER. The excretion of carbon dioxide by frog nerve. Journ. of general physiology, Sept. 1925.

[4]) The horizontal cells in the embryonic cortex establish the only exception, but these disappear later.

earlier ontogenetic outgrowth, a consequence of its greater susceptibility to the activating impulses (fig. 7).

Another difference between the neurite on one hand and the cell body and dendrites on the other is their opposite neurobiotactic response to the nervous current, the neurite growing in the same direction as the current, the dendrite and cell body growing or shifting in the opposite direction, approaching the source of the nervous impulse (stimulation centre, Fig. 5).

A striking fact with neurones is also that the *interneuronal link* transmits only in one direction, even experimentally. We call this the *synaptic condition* of the neuronic chain.

After what has been said concerning the ambiconductive capacity of both sorts of offshoots, it is evident that this synaptic condition cannot be due to a monoconductive character of each offshoot as a whole.
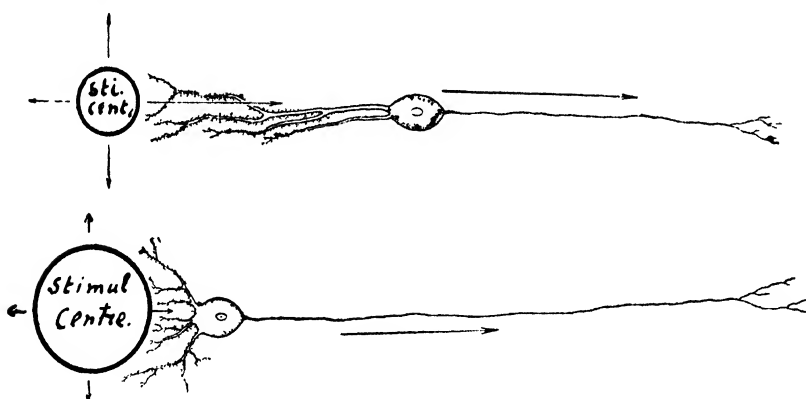

Fig. 5. Polarized neurobiotactic differentiation of the neurone.
The arrows indicate the course of the impulse.

We do not know the exact cause of the monoconductive character of the synaps, but it may be that the opposite reactions of neurites and of dendrites to the stimuli that influence them during their development, may shed some light on it. For this the *neurobiotactic polarization* must be considered more amply.

As the neurosensory cell has no dendrites but only a neurite, so the *neuroblast* from which the neurone develops forms only a neurite at first. This apparently arises from a protoplasmatic

substance which follows the direction of the stimulation or action current, which enters the cell at one side and leaves it at the other. The
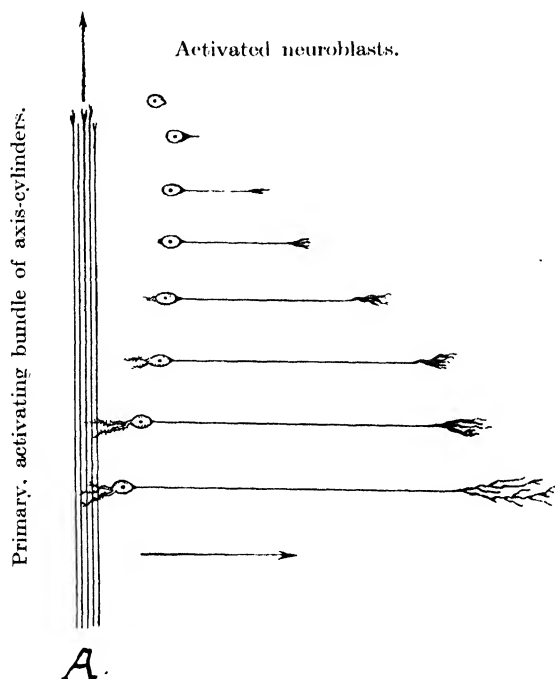

Fig. 6. The activation of neuroblasts by an amyelinated, growing bundle of nerve-fibres (Bok). The vertical arrow indicates the direction of the growth and of the stimulation current in the primary, activating bundle. The horizontal arrow indicates the direction of the radiating impulses.

neurite grows with this outgoing current, thus assuming the same direction of the action current. Its growth is *stimulo-concurrent* (KAPPERS), starting at the side of the neuroblast opposite to the receptive surface. This also appears from BOK's[1] researches who saw that the motor neuroblasts of the chick embryo develop their neurite away from the still growing nerve fibers of a bundle which runs along behind them. The irradiating influence of this "activating" bundle apparently causes the neuroblasts to grow a neurite, as the neurites appear

---

[1] Bok. Die Entwicklung der Hirnnerven und ihrer zentralen Bahnen. Folia Neurobiologica, 1915.

only in such neuroblasts as are passed by the activating bundle.

It is only a good deal later, about the time when tigroid substance appears (CAJAL) that the ordinary cytoplasm of the cell grows out in dendrites. But this cytoplasm (tigroid specially) has an opposite potential and consequently extends itself in an opposite direction, viz. *to* the source of the activating current: *stimulopetal*. The homogeneity of the dendrites and ordinary cell protoplasm is shown again by the fact that the cellbody also may now shift in a stimulopetal direction[1]) (fig. 5).
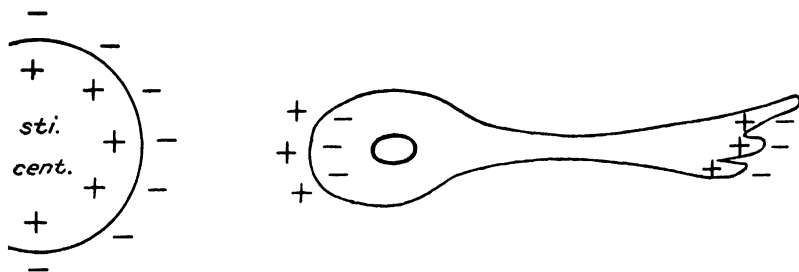

Fig. 7. Attempt to¶locate the potentials in a stimulated activating bundle and neuroblast. Action current and outgrowth probably involve potassium ions (+).

That this opposition of growths bears a great resemblance to polarized growth in an electric field is made probable by the work of KAPPERS (l. c. 1917), INGVAR [2]), CHILD [3]) and KELLER [4]).

Now these differently polarized parts of two nerve cells touch each other in the synaps. On account of this it seems quite possible that a semipermeable double layer is formed here through which a transmission can occur of only such a current as accords with the bioelectric stimuloconcurrent character of the neurite and the stimulopetal bioelectric nature of the cellbody or dendrite.

Consequently, although both neurite and dendrite, because of the fact that each of them is everywhere *homogeneous*, may conduct

---

[1]) It may be added that the neuroblast itself, as long as it has not developed Nissl substance may also shift with the current.

[2]) INGVAR. Reactions of cells to the galvanic current in tissue cultures. Proc. of the American Soc. of Experin. Biol. and Med. Vol. 17, 1920.

[3]) CHILD. The origin and development of the nervous system. University of Chicago press, 1920.

[4]) KELLER, Die Elektrizität in der Zelle, Braumüller, Wien, 2d Ed. 1921.

in either direction (if stimulated in the midst of their course) it is quite possible that where their heterogeneously polarized surfaces touch each other, a transmission can take place only in a direction compatible with their opposite polarization.

This, in my opinion, is the most probable explanation of the monoconductive transmission at the synaps. I consider it a consequence of the contact at this point between neuronic endings each of which are polarized in one direction only [1]). If this explanation is correct *the polarization and the synaptic character of the neurones both are phases of the process of neurobiotaxis.*

This endeavour to explain the irreversible character of the interneuronic link by the opposite polarized characters of the neuronic parts which meet at the synaps does not necessarily exclude the possibility that at the interneuronic link some special arrangement may be present (SHERRINGTON). But a special junctional substance has never been observed between neurones, whose fibrillae are even often continuous (OUDENDAL, MARUI, BIELSCHOWSKY and WOLFF).

Other characteristics of the synaps, — the retardation in the nervous transmission, and its susceptibility to fatigue and to special drugs, may be due to the fact that the fibrillae of the telodendria (endfeet of AUERBACH) split in very fine branches, closely surrounded by a glious network that easily reacts to fatigue (MARUI) and also to drugs and then may secrete toxins that are noxious to the synaps.

So much concerning neurobiotactie polarization. Another neurobiotactic phenomenon, the tendency of simultaneously stimulated nervecells (or offshoots) to join, will be frequently illustrated in the following text (page 28, 29, 45 a. f.).

Origin of the neurone. The myeline sheath.

Genetically, neurones nearly always arise from superficial epithelial cells (placode cells) or from deeper cells of epithelial origin (neuroblasts). They apparently are more closely allied to neurosensory cells than to primitive ganglion cells.

---

[1]) In this connection I also refer to LILLIE's experiments. Passive iron, when touched by ordinary active iron becomes active, also acquiring a wave of negative potential, the negative potential of one part activating the other. Between passive iron and passive nickel the wave is only transmitted from the nickel to the iron, not vice-versa.

One reason for this supposition has already been mentioned, viz. that *the neurosensory cell also has a polarized conduction*, on account of its special position.

Against the objection that the neurosensory cell is merely sensory and never motor in character, as are many neurones, may be advanced the fact that neurosensory cells also occasionally terminate in muscles, as observed by HAVET and HESS in worms, (p. 31) by SAMASSA in the tentacles of Helix (see p. 39).

This proves that the neurosensory cell may combine all the functions of neurones, receptive, conductive and effective, as has been already pointed out by DROOGLEEVER FORTUYN. Furthermore it has been proved that the cranial ganglia and their neurones in vertebrates, though largely arising from neural crest cells, originate partly as placode cells, viz. as epithelial cells in the skin, closely resembling embryonic neurosensory cells.

Moreover, although the neurosensory cell generally has no receptive offshoots, the cell (and sense hair) being the only receptor, HAVET has found in Worms, and VERATTI in Gastropods (see fig. 20), neurosensory cells under the epithelium having long peripheral offshoots branching in the epithelium, so that practically no difference from sensory neurones could be stated.

Nevertheless branching receptive elongations of neurosensory cells are rare and are limited to a few cases. On the other hand, the dendrites of neurones are remarkable for their length and multiplicity; they enable impulses from several directions and sources to enter the neurone, which thus becomes a "common path" and correlator of various impulses.

Thus neurones may act as typical instruments of correlation.

As already stated above their neurite, exceptionally also the dendrites (sensory nerve roots) may be surrounded, by a myeline sheath. This sheath like arrangement of myeline enhances the rate of conduction that may increase to 125 M. per sec. in myelinated nerves.

The influence of the development of the myeline sheath on conduction is probably due to two factors, chiefly to elimination of the poorly conducting lecithine, while secondly the myeline sheath itself (according to GÖTHLIN [1]) by piezo-electricity) may strengthen the current.

---

[1]) GÖTHLIN. Die doppelbrechenden Eigenschaften des Nervengewebes. Kungl. Svenska Vetenskapsakademiens Handling. Bnd. 51, 1913. and Relation entre

Myeline serves, moreover, as an *insulator*, preventing by its poor conductivity the nervous current from radiating sideways as may occur in naked neurites (for the functional significance of these radiations, see the parallel fibers in the cerebellum).

The elimination itself of the myeline from a neurite is a consequence of perpendicular radiation, as appears from the fact that in young neurones the myeline micelli (liquid cristals) are arranged with transverse optic axes, while in the sheath their optic axes are arranged paralel to the neurite (VALENTIN), i. e. transverse on the radiating current, that they oppose. Their poor conductivity which in unsheathed fibers lowers the rate of conduction, in sheathed fibers prevents a sideway outflow, the more so, as the myeline increases by additions from sheath cells.

Hence, by their greater rapidity of conduction and better insulation, neurones are typical constituents of higher nervous organisations.

Moreover the peripheral neurones (also those without myeline sheath) are surrounded by lemnoblasts, (cells of SCHWANN), which may also occur round the neurites of neurosensorycells, (the fila olfactiva for instance) but are not observed in this arrangement around primitive ganglion cell offshoots.

Neurones do not yet occur in Coelenterates. They are found first in *flatworms*. Becoming much more abundant in the higher invertebrates, they form the great majority of nerve cells in vertebrates, where the neurosensory cells, which are the prevailing sensory recipients in invertebrates (see fig. 17) are restricted to the eyes and the olfactory epithelium. Primitive ganglion cells, so abundant in invertebrates, in vertebrates are found in the peripheral parasympathetic [1]) system, in the plexus of MEISSNER and (partly) in the plexus of AUERBACH. That visceral regions keep a primitive type of nervous organisation, is not strange, since their impulses as well as their motor activities only involve a very simple type of nervous action. Even its rate of conduction is similar to that in the ganglionic plexus of coelenterates (20 c.m. per sec.; ALVAREZ [2]) and the current may run in both directions here.

le fonctionnement et la structure des éléments nerveux, Upsala Läkere förenings Förhandlingar, Bnd. XXII, 1917.

[1]) The amacrines in the optic lobes of Octopods and Insects and in the retinae of Vertebrates also resemble primitive ganglion cells.

[2]) ALVAREZ. The mechanism of the digestive tract. New-York, 1922.

THE NERVOUS SYSTEM OF INVERTEBRATES.

Coelenterates.

In the zoological system nerve cells first occur in the *Coelenterates*, and the arrangement of these cells in the various groups of this class has been a much discussed subject ever since KLEINENBERG [1]) and the HERTWIGS [2]) made their fundamental observations.

Referring for a historical sketch of the literature up to 1920 to FORTUYN's [3]) extensive survey, I shall briefly describe the structure of the nervous system in these animals as it has been revealed in more recent years by the chromesilver and mythelene-blue methods, by ZOJA [4]), HAVET [5]), WOLFF [6]), GROSELJ [7]), PARKER and TITUS (l.c. infra) and SCHULZE.

Only two sorts of nerve cells may be distinguished here: *neurosensory cells* and *primitive ganglion cells*.

---

[1]) KLEINENBERG. Hydra, 1872.

[2]) O. & R. HERTWIG. Das Nervensystem und die Sinnesorganen der Medusen 1878, and

Die Actinien; Jenaïsche Zeitschr. Naturw. Bnd. 13, 1879, and Bnd. 14, 1880.

[3]) DROOGLEEVER FORTUYN. Die Leitungsbahnen im Nervensystem der Wirbellosen, Bohn, Haarlem, 1920.

[4]) ZOJA. Alcune ricerche morfologiche e fisiologiche sull'Hydra, Dissertazione, Pavia, 1890. The same. Sugli trasmissibilità degli stimoli nelle colonie di Idroidi. Re. Conto dell'Instituto lombardo. vol. 24, 1892, p. 1225 and Intorno ad alcune particolarità di struttura dell'Hydra, Ibidem Vol. 25, 1892, p. 709. A short resumé of his results is published in the Zool. Anzeiger Jahrg. 15, 1892.

[5]) HAVET. Contribution à l'étude du système nerveux des Actinies. La Cellule 1901, Tome 18.

HAVET. La structure du système nerveux des Actinies. Leur mécanisme neuro-musculaire. Libro en honor de D. S. Ramon y Cajal, Tomo I, 1922.

[6]) WOLFF. Das Nervensystem der Polypoiden Hydrozoa und Scyphozoa. Inaugural Dissertation, Jena, 1903, published in the Zeitschr. f. allgem. Physiologie, Bnd. 3, 1904.

[7]) GROSELJ. Untersuchungen über das Nervensystem der Actinien. Unters. Zool. Inst. Wien, 1909, Bnd. 17.

Neurosensory cells are very abundant in Coelenterates, in the ectoderm as well as in the entoderm, thus showing that nervous elements may arise from both.

Their cellbodies lie in the epithelial layer (see fig. 1). Usually, though not always, a hair like offshoot (sense hair) extends over the surface, while the basal elongation of the cell, the neurite, runs in the underlying tissue, where it often dichotomizes. It generally ends near the base of the epithelium in which its cell body lies, but some neurosensory cells in the entoderm of anemones send their neurites to ganglion cells lying near the muscles of the ectoderm (HAVET, PARKER and TITUS) and there are even neurosensory cells in the tentacles of Hydroids and Cerianthus (GROSELJ), whose neurites run to the ganglionic plexus at the bases of the tentacles [1]).

The neurites of neurosensory cells in Coelenterates always terminate in a primitive ganglioncell plexus. Direct endings of neurosensory cell neurites in muscles, as observed in Molluscs have not been seen with certainty in Coelenterates, although they are supposed by PARKER and TITUS to occur in the tentacles of Metridium. Similarly CITRON [2]) supposes that the *palpocil cells* on the tentacles of Hydra (fig. 7) are neurosensory cells whose neurites end in muscle tissue.

As already stated, in most Coelenterates these cells are very numerous in the entoderm as well as in the ectoderm.

An interesting exception is found in Hydra, where neurosensory cells are very rare in the ectoderm. This fact is explained, by SCHNEIDER and WOLFF, by the enormous proliferation of *cnidocil apparatuses*, which, though present in nearly all Coelenterates are especially abundant in the ectoderm of this animal. This leads us

---

[1]) HICKSON saw ganglion cells in the mesogloea under the ectoderm of the tentacles in Alcyonium digitatum (vide The anatomy of Alcyonium digitatum, Quarterly Journ. of micr. Science. Vol. 37, 1895) and ASHWORTH did the same in Xenia Hicksonii (Quarterly Journal of microsc. science, vol. 42, 1899) but in Actinia, according to Havet, Parker and Titus - - the tentacles themselves contain no ganglion cells. Wolff, however, draws ganglion cells in the tentacles of Actinia and also of Hydra, but not in those of Hydrophaena fig. 7).

[2]) CITRON. This author saw them in Syncoryne Sarsii. See Beiträge zur Kenntniss des Syncoryne Sarsii. Inaug. Dissertation. 1902.

to suppose that the function of reflectory defensive response
(and offence) is largely carried out by cnidocel cells in the ectoderm
of Hydra.

This system may serve for both, perception and defence, being
a very sensitive reflectory apparatus.

The *cnidocil cell* (or *nemato-cyst*) is provided with a very sensitive
hair, which, after being touched, may cause a thread — a microsco-
pical harpoon — to be protruded suddenly by the cell; this injures
the offender, the more so since this mechanical reflex is usually
combined with the secretion of a poison well known to swimmers
who have been in contact with jellyfish [1]).

HERTWIG, VON LINDENFELD, GROSELJ and some others believe that there
are cnidocil cells which have long basal offshoots joining the ganglionic
plexus. HAVET's pictures (1922) also show very long basal offshoots from such
cells. HAVET, however, has given considerable attention to this question,
and is inclined to consider these offshoots as non-nervous. (See note 1).

These nematocysts are supported by, and even sometimes im-
bedded in epithelio-muscular cells.

Primitive *ganglion cells* immediately underneath, and even partly
in the ectoderm, seem to send offshoots between these epithelio-
muscular cells and, according to several authors, also to the nema-
tocysts. That the cnidocil apparatus, consisting of a nematocyst and
one or more supporting muscle cells, may be innervated by a primi-
tive ganglioncell, has been first observed by DANIELSSEN [2]), DELAGE
and HÉROUARD [3]).

ZOJA and WOLFF even maintain that one offshoot of such
a ganglioncell may be connected with the vesicular nematocyst

---

[1]) Sometimes even cnidocil cells seem to injure their own host. Thus
PARKER and TITUS (l. c. p. 445) saw cells of the acontium which had
discharged their cnidocil in the neighbouring mesenteries. Whether the
figures of HAVET (La Cellule, Tome 18. p. 393) must be explained by such
cells having turned top to bottom, discharging their threads into the mesoderm,
as HAVET supposes, I do not know.

[2]) DANIELSSEN. Actinidae of the North Atlantic expedition. Bergens Museum
Aarbog, f. 1887.

[3]) DELAGE et HÉROUARD. Traité de Zoologie concrète. Les Coelenterées
(Pl. I, fig. 2). Paris 1901.

itself [1]), while another offshoot ends in the contractile foot of the epithelio-muscular cell in which the nematocyst is imbedded, and in other adjacent epithelio-muscular cells.

If such a primitive ganglion cell, connecting nematocysts and
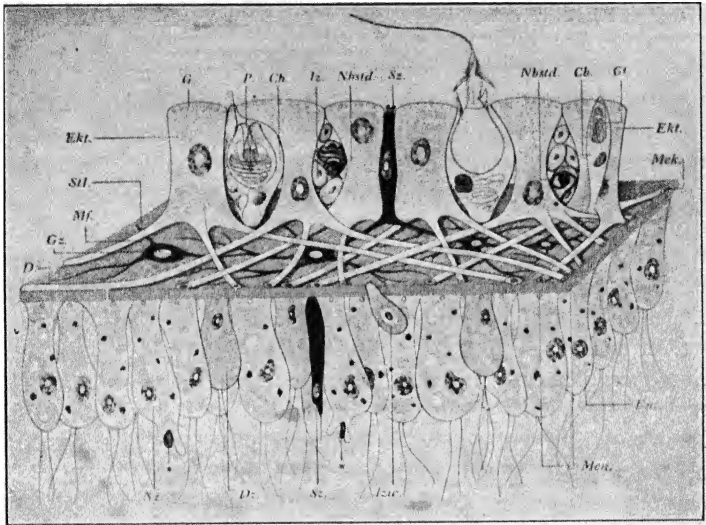

Fig. 8. Organisation of the mantle of Hydra, after SCHULZE.
Ekt. = ectodermal epithelium; G = epithelio-muscular cell of which Mf. is a muscle fiber; P = penetrating cnidocil cell with Cb. = cnidoblast; Iz. = interstitial cell; Nbstd. — capsular cell; Sz. = neurosensory cell; Gt. — glutinant cnidoblast; Mek. = ectodermal muscle-layer; Stl. = mesogloea (layer between the ectoderm and entoderm) Gz. = primitive ganglioncell (black); Nz. = Nutritive cell; Dz. = glandular cell; Sz. — neurosensory cell; Izw. = interstitial cell; Men. = muscle fibers of the entoderm (Ent.).

epithelio-muscular cells, also sends an offshoot to the deeper ganglionic plexus, it would combine an intraepithelial reflectory function with a deeper conductive function, and thus explain the

---

[1]) SCHULZE however denies this connection of cnidocil cells with ganglion cells (see BROHMER, EHRMANN und ULMER. Die Tierwelt Mittel-Europas, Teil I, Heft 1, 1928).

scarcity of neurosensory cells, so abundant in the ectoderm of most Coelenterates, in the ectoderm of Hydra.

This connection of nematocysts with ganglion cells is certainly no rule, nor is it necessary.

As the nematocyst is located in or between epithelio-muscular cells, this contact may be sufficient to transmit the impulses which it receives to the surrounding epithelio-muscular cells. This is made probable by the fact that not all (though many [1])) cnidocil apparatuses are connected with a ganglion cell. It has, moreover, been shown (PARKER [2])) that a cnidocil apparatus may function without the interference of primitive ganglion cells, which may be anaesthesized without the cnidocil function being affected.

From this fact we may conclude that the connection with a ganglion cell does not introduce a new function, but integrates a preexisting one. This integrative action may have the following advantages:

The conduction of stimuli runs more quickly by means of a ganglion cell [3]).

The ganglion cell may reinforce the stimulus by adding stored energy of its own.

The ganglion cell plexus is but slightly subject to fatigue. This was clearly shown by MAYER [4]) and HARVEY [5]) who caused a nervous current in a closed ring of tissue cut from the jellyfish Cassiopea to run continually for eleven days, covering 537 miles. It was stopped only by counteracting impulses from regenerating tissue.

The conduction may spread over a wider area, since we know that most ganglion cells carry the impulse not only to one effector, but generally to many by means of the deeper lying ganglion cell plexus.

---

[1]) According to ZOJA (l. c. p. 707) not only the large cnidocil cells (his macrocnidi) but also the smaller ones (microcnidi) show this arrangement in Hydra, and WOLFF found it also in Actinia.

[2]) PARKER. Effector system in Actinians. Journ. of Exper. Zool. Vol. 21, 1916.

[3]) This was shown by PARKER. The circular muscle of the columnwall of Metridium may act as well by direct stimulation as by the interference of nerve cells. In the latter case the motion is propagated faster.

[4]) MAYER. Rythmical pulsation in Scyphomedusae I and II. Carnegie institution publications No. 47, 1906 and No. 102, 1908.

[5]) HARVEY. Some recent experiments on the nature of the nerve impulse. Journ. of Nervous and mental disease. Vol. 55, 1922.

Thus, we find the *integrative action of the nervous system,* so emphasized by SHERRINGTON in his fundamental book of this name, to be evident in the earliest nervous organisation.

Whereas the basi-epithelial ganglion cells lying immediately under the epithelium and partly between its feet, may represent the most primitive cells of this type, other primitive ganglion cells lie a
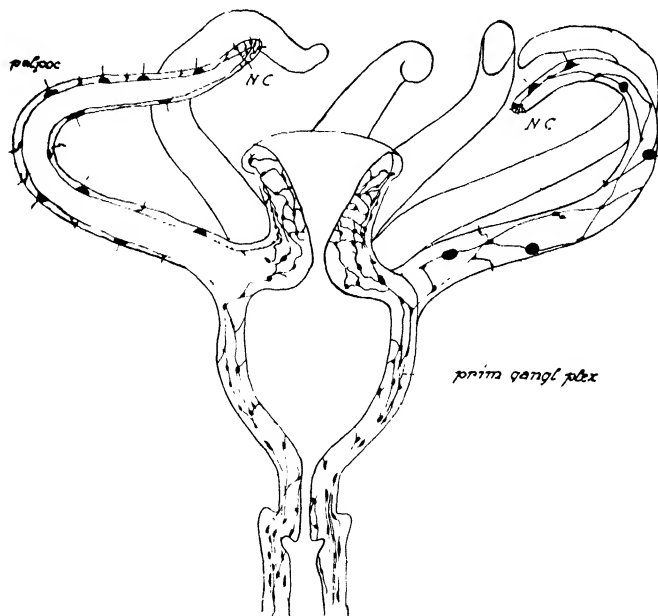

Fig. 9. Nervous system of a hydrant of Hydrophaena, after WOLFF. The tops of the tentacles show many neurosensory cells (N.C.). The large dots represent palpocils. The primitive ganglion cell plexus is especially well developed round the mouth.

little deeper in the mesogloea. They are however connected with the basi-epithelial plexus.

That all the ganglion cells in Coelenterates are unpolarized does not seem to be absolutely settled. Those in the deeper plexus certainly may conduct in both directions. It is however possible that ganglion cells with endings in the epithelium lead in one direction only, viz. from the surface to the muscle fibers and therefore, such

cells may perhaps be more or less allied to neurones, although histologically they still resemble primitive ganglion cells.

Finally, it should be noted that in Hydroids the nervous system of the hydranths is connected with that of the stem or hydrocaulon (see fig. 9), but that the stronger impulses only may pass from the hydranths to the stem (WOLFF, l. c. p. 52).

This may be explained by the larger number of primitive ganglion cells intercalated in longer distances. Thus, also, one tentacle may be stimulated to movement, without influencing another, provided the stimulus is low.

Fig. 9 shows the simple arrangement of the nervous system in a Hydroid (Hydrophaena). In such sessile coelenterates no special sense organs as light percipient cells or statocysts occur (c.f. p 72).

In the swimming Medusae the nervous system is more differentiated. Near the place where the velum joins the umbrella one or two ganglionic rings occur, acting a part in the swimming movements. Another complication is introduced here by sense organs, the *statocysts* and the *eyes*.

The former are located under the umbrella, near the radial and interradial channels and consist of statoliths resting on ciliated neurosensory epithelium, which extends beyond the statoliths into "sensory furrows". Under the epithelium of the inner furrow more ganglion cells are accumulated than in other places HESSE [1]) and BOZLER [2]) consider this to be the centre for static impulses, which run from here into the *subumbrellar ganglionic ring* and influence the rythmic heartbeat like swimming movements.

The eyes of the Medusae are also located under the umbrella near the statocysts and their neurosensory cells also enter a ganglionic plexus. The function of these eyes is to permit orientation to light, just as the statocysts subserve orientation to gravity, light and gravity being the chief forces for the orientation in space of such animals.

Other accumulations of primitive ganglion cells occur around the mouth. This concentration is, however, a common feature of all Coelenterates.

---

[1]) HESSE. Das Nervensystem und die Sinnesorgane von Rhizostoma. Zeitschr. f. wiss. Zoöl. Bnd. 60, 1895.

[2]) BOZLER Sinnes- und nervenphysiologische untersuchungen an Scyphomedusae. Zeitschr. f. vergl. Physiologie, Bnd. 4, 1926. —

Echinoderms.

The nervous system of Echinoderms resembles that of Coelenterates in consisting only of neurosensory cells and primitive ganglioncells. It differs from it by the fact that in the addition to the *basi-epitheleal plexus* (outside the calcareous layer), innervating, inter alia, the muscles of the spines, it contains *deeper radially arranged strings*.

In this deeper system two divisions occur, between which no histological connections have been observed, though morphologically (vide infra) and physiologically (PLATE) there are arguments in favor of such connections. These are the *ectoneural* and *hyponeural systems*, in addition to which, in Crinoids only (fig. 8), an *apical* system occurs.

The ectoneural system arises from the ectoderm and remains near the epidermis (fig. 10). The hyponeural system originates from the coelomic wall (thus not being ectodermal in origin). The *ectoneural system* is arranged around the mouth as a ring, from which branches (ectoneural radial nerves) continue under the ventral epithelium of the arms. It acquires a deeper position only in Ophiurids, Echinids and Holothurians, where it lies at the bottom of the ectodermal canal which arises from the closure of the ambulacral furrow.

There are some local accumulations in it, especially at the bases of the ambulacral feet, which are very sensitive and contain a large number of neurosensory cells, sending their neurites to the underlying ganglion groups. The latter also contain motor cells for the pedal muscles (HAMANN) and others connected with the muscles of the spines.

Although primitive motor ganglion cells do occur in the ectoneural system (around the mouth also) its great content of neurosensory neurites shows that it sensitive functions are many. So also the *static organ* of Echinids (consisting of neurosensory cells) sends its neurites in the ectoneural system.

The second, or *hyponeural system*, arising from the coelomic wall, also lies near the mouth (without however forming, a closed ring). From here *two* hyponeural radial nerves (fig. 10) extend into each arm.

Although the origin of the hyponeural system is different from that of the ectoneural, these systems sometimes lie close together.

This is especially the case with Ophiura, where their circumoral parts have closely approached each other, while their radial nerves almost form one string, in which the two divisions are separated only by a thin lamella of connective tissue (TEUSCHER).
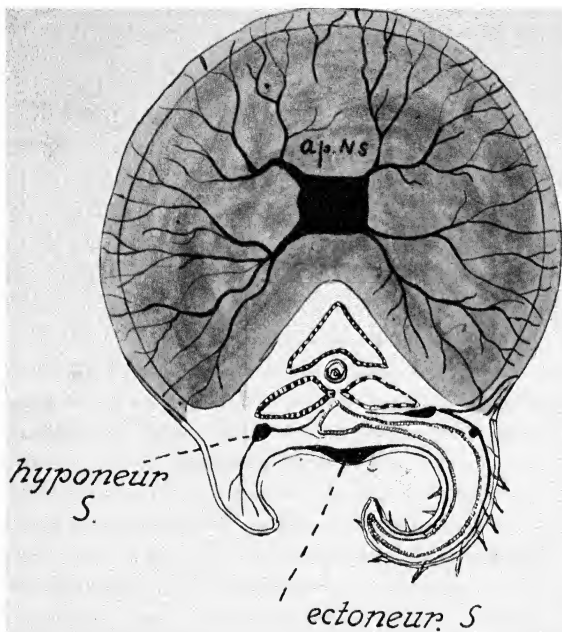
Fig. 10. Arrangement of the ectoneural, hyponeural and apical nervous systems in an arm of a Crinoid, after LANG.

This close morphological relationship is, perhaps, an indication of a functional correlation, although no fiber connections between the plexuses have as yet been observed.

In contrast to the ectoneural system, the hyponeural contains a great many *motor primitive ganglion cells* scattered among its fibers, and connected with muscles (HAMANN).

LANGE [1]) has also observed more concentrated ganglia in it, in Asteroids, lying immediately underneath the *eyes* at the end of each arm. These ganglia receive the neurites of the light percipient cells [2]).

Connected with the hyponeural system, and of similar origin, is the *apical or dorsal system*, which does not occur in all Echinoderms but which, in *Crinoids* (fig. 10), surpasses the other systems in size.

---

[1]) LANGE Beitrag zur Anatomie und Histiologie der Asteriden und Ophiuren. Morph. Jahrbuch Bnd. 2, 1876.

[2]) Whether the ectoneural system also carries neurites of light percipient cells is not yet settled.

It surrounds the so called dorsal fanlike organ, consisting of nerve fibers in which bipolar and multipolar primitive ganglion cells are scattered.

Peripheral branches of this system are connected with the muscles of the arms, the cirrhi and the peduncle of the crinoid body. It also receives offshoots from neurosensory cells in the skin. Ventrally, its fibers are connected with the hyponeural plexus. (LUDWIG and HAMANN) [1].

The apical system is further remarkable in the fact that between the two branches into which the apical radial nerves divide peripherally very regular commissural and decussating bridges occur. This seems to be an expression of interaction among the plexuses of the arms without the interference of the body plexus, which would not be astonishing, since local reflexes are frequent in Invertebrates (c. f. also p. 38—39 and 49).

The nervous system of Worms. General arrangement.

In the nervous system of both groups, in which the worms are divided, the Scolecids and Annelids, we may distinguish two parts, a superficial plexus and a stringlike deeper or central nervous system; the two are, however, intimately connected.

The *basiepithelial plexus,* of flatworms like the superficial network of Coelenterates, consists of offshoots of neurosensory cells and primitive ganglion cells, forming a *ganglionic plexus* which also resembles the Coelenterate network in that it consists mainly of *single* threads and cells, fiber *bundles* being very rare in it. It differs from the Coelenterates, by the occurrence of *bipolar neurones* which, however, are still very few in flatworms but numerous in higher worms.

In the higher Scolescids and in Annelids the basiepithelial plexus is reduced, but the intramuscular plexus is still considerable and contains *fiberbundles* among which cells occur.

The *central nervous system* ontogenetically also arises from epithelial cells, but shifts much deeper than the peripheral plexuses, finally acquiring a position under the skin musculature, and in

[1] LUDWIG and HAMANN. Crinoidea in Bronn's Klassen und Ordnungen des Tierreichs Bnd II, Abt. III, Buch 5, 1907.

Comp. also DROOGLEEVER FORTUYN. Die Leitungsbahnen im Nervensystem der Wirbellosen Tiere. Bohn, Haarlem 1920.

higher worms passing through the coelomic cavity, where it is arranged in parallel longitudinal strings, or *connectives*, meeting in front of the mouth in a more concentrated knot: the *cerebral ganglion* (fig. 11 and 12) a result of the great exposure of the head to stimuli.

The deeper nervous system is characterized by *accumulated bundles* of fibers and clusters of primitive ganglion cells, and contains many *unipolar neurones*.

In the most primitive flatworm, *Planocera*, this accumulation into longitudinal strings is still poorly expressed (fig. 11), and the connectives still lie near the skin muscles (PLATE [1]) and v. GRAFF [2]). Thus, the nervous system of this animal, although its connectives consists of real *bundles*, not of *single* fibers and cells only, still closely resembles that of the Coelenterates.

In the *Acoela* (fig. 12), which in some respect represent the next higher stage, the longitudinal arrangement of the strings is more obvious, but their number is still large, generally six, three on each side, a ventral, a lateral ,and a dorsal pair. This number may even increase to 4--6 pairs (PLATE) so that the concentration is still little advanced.

An interesting fact, mentioned by PLATE, is that in swimming representatives of the Acoela the dorsal strings are more developed, while in the crawling representatives of this group the ventral pair is thickened. I am inclined to believe that the preponderance of the ventral pair is due to the influence of ventral impulses and effectors.

In *Turbellaria* and *Trematodes* the ventral pair of connectives is by far the strongest (see Harmostomum, fig. 13). Also here the accumulation in the ventral pair of strings is apparently due to the prevailing importance of the ventral side of the body in sensory and motor functions. Trematodes are provided with large adhesive discs which, located ventrally, have an abundant sensory and motor innervation and in *Turbellaria* the ventral surface of the body contains more sensory cells than the dorsal [3]).

---

[1]) PLATE. Allgemeine Zoologie. Teil I, Fischer, Jena, 1922, p. 392—394.

[2]) v. GRAFF. Turbellaria in BRONN's Klassen und Ordnungen 1904--1908, Acoela, Engelmann, Leipzig, 1906. Quoted after PLATE.

[3]) HANSTRÖM Ueber den feineren Bau des Nervensystems der tricladen Turbellarien. Acta Zoologica, Bnd. 7, 1926.

Arrangement of the nervous system in some flatworms.
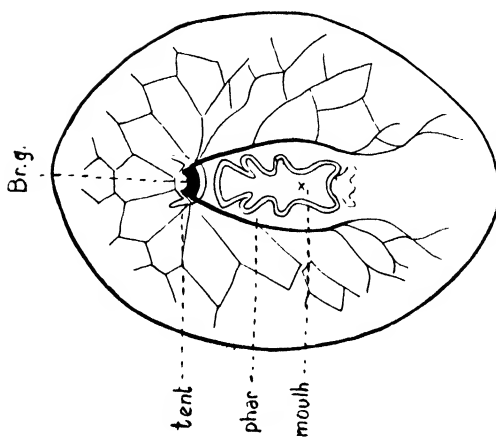
Fig. 11. Nervous system of Planocera after LANG (taken from PLATE). Br.g. = brain ganglion; tent = tentacle; phar. = pharynx.
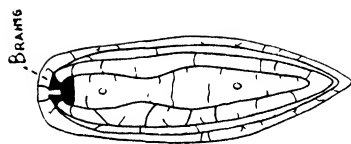
Fig. 12. Dorsal aspect of the nervous system of a swimming Acoel (Convoluta roscoffensis) after v. GRAFF.
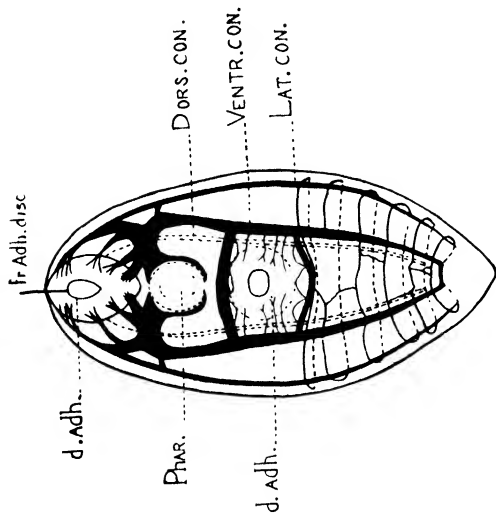
Fig. 13. Ventral aspect of a Trematode, Harmostomum lept. after BETTENDORF (from PLATE). The two adhesive discs are strongly innervated by the ventral string. Ventral and thinner lateral strings in black. Dorsal string dotted.

The *Nemertini* also have large ventral strings and in some of them the deeper nervous system also lies nearer the intestinal tract.

In this respect and by the greater differentiation of their nervous elements, they resemble the segmented worms, or Annelids.

In the segmented worms, Annelids, the deeper nervous system is concentrated in one pair of strings: the ventral connectives.
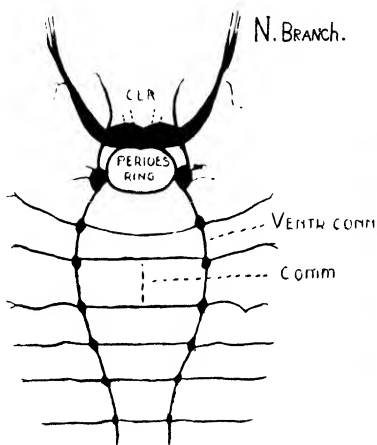
Fig. 14. Nervous system of a lower Annelid, Serpula fascicularis, after DE QUATREFAGES.
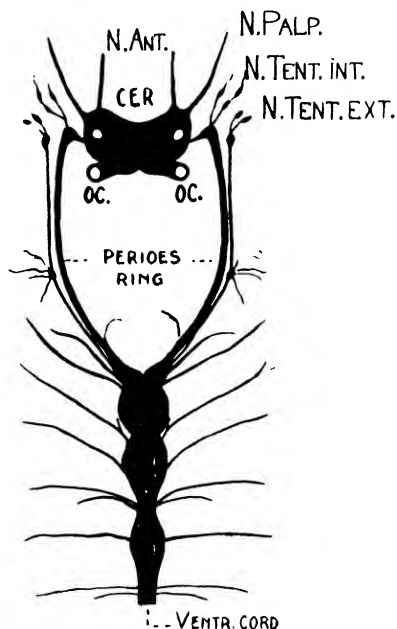
Fig. 15. Nervous system of a higher Annelid, Nereis regia after DE QUATREFAGES. (cf. fig. 17.)

In every segment transverse commissurs located between the ganglionic knots connect the strings. These commissures are doubtless a product of the simultaneous nervous action on both sides of each segment, and their formation thus is an example of that phenomenon of *neurobiotaxis* so often observed in vertebrates: the outgrowth of nerve fibers between simultaneously functioning

centres. Such centres then have a tendency to approach each other, as is also observed with the ganglionic knots in Annelids compare fig. 14 with fig. 15).

So, though the ventral cord of these animals is generally referred to as the *ropeladder nervous system,* and retains this character in some species (fig. 14), in most of them the resemblance to a ropeladder
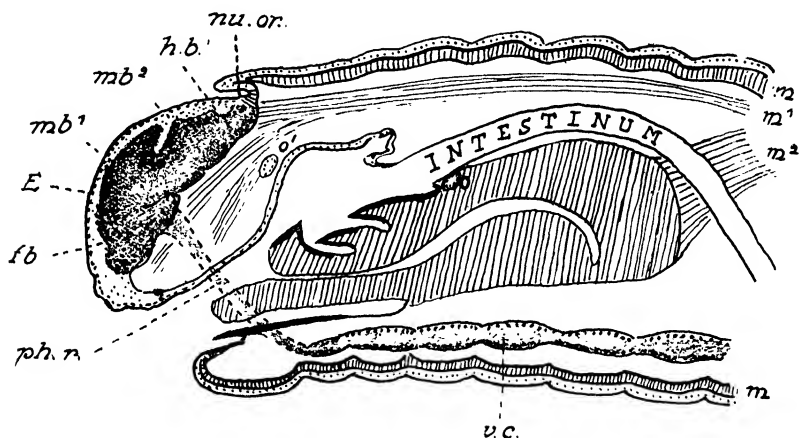
Fig. 16. Paramedian section of the frontal part of Eunice punctata after HEIDER, showing the close relationship of the brain with the ectoderm of the prostomium (E). The brain shows a division in a forebrain (f.b.), two midbrains (mb¹ and mb²) and a hindbrain (h.b.) near the nuchal organ (nu.or.). m = circular musculature; m¹ = longitud. musculature; m² = jaw musculature; o and o¹ = inferior and superior buccal ganglion; ph.r. = pharyngeal nerve ring (schematic); v.c. = ventral cord.

is veiled by the fact that the longitudinal strings run very near each other, and often join (fig. 15), this process being introduced by a junction of their ganglionic knots.

The transformation of the ventral pair of connectives to one *ventral cord* may be completed by the formation of a common sheath of connective tissue, more or less comparable to the meningeal tissue of the vertebrates.

The ventral position of the cord is the result of the fact that this side is the most stimulated and most active side in annallid ancestors, since ganglion cells tend to develop near, or shift toward places which are most stimulated (neurobiotaxis).

In contrast to the cord, the *headganglion* develops *dorsally* from the dorsal epithelium of the prostomium, the region in front of the mouth being very much exposed by forward locomotion.

In many forms, as Eunice, (fig. 16) it retains a close contact with the ectoderm. The ganglion is usually divided into three parts, each of which is closely related with special sense organs. The "forebrain" is connected with the very sensitive palpi the motor innervation of which also depends on it. The "midbrain" (often divided into two parts) is connected with the lateral antennae and the eyes, and the "hindbrain" with the impair antenna and the nuchal organ, which is considered, by some authors, to be an olfactory organ.

From these facts it is evident that the dorsal development of this ganglion is due to the dorsal location of the chief sense organs of the head.

The head is the most sensitive region. Next comes the tail region, which contains more nerve cells than the more protected middle part of the body, and in higher worms also contains large reflectory cells (p. 36). Similar relations are observed in Amphioxus (pag. 78).

The histology of the nervous system in worms.

The *peripheral plexus* of *Scolecids* chiefly consists of primitive ganglion cells, especially in flatworms (EHRLICH). In addition it contains neurites of neurosensory cells lying in the skin, and some bipolar *neurones* (MONTI [1])) whose cell bodies lie in the muscle layer, while their dendrites end in the skin. The neurites of the latter, however, in most cases finally enter the connectives as do most neurosensory neurites.

In the adhesive discs of Trematodes (fig. 13) the superficial plexus is further differentiated consisting of a peripheral layer containing nerve cells, and a deeper one containing only fibers (BETTENDORF [2]). The former is considered to be more sensory in function, while the fiber layer contains neurites of central motor cells.

---

[1] MONTI. Sur le système nerveux des Dendrocèles d'eau douce. Arch. Ital. de Biologie, Tome 27, 1897, and Nuove recherche sul systema nervoso delle planarie. Monitore Zool. Vol. II, 1900.

[2] BETTENDORF. Ueber Musculatur und Sinneszellen bei Trematoden. Zool. Jahrb., Bnd. 10, 1897.

In Trematodes also subepithelial neurosensory cells occur with more than one peripheral branch, thus resembling the dendrites of bipolar neurones (HAVET). The subepithelial and intramuscular plexuses of *Annelids*, recently studied by DAWSON [1]) and HESS [2]), contain several neurones in addition to primitive ganglion cells and collateral neurites of neurosensory cells.

Their intra-muscular plexuses contain cells which have a bipolar character, being probably migrated neurosensory cells. Other, (tripolar) cells, lying in the muscle tissue, are considered by DAWSON to be effector cells. However, their terminations in the muscles have not been seen, their offshoots passing mostly into the basie-epithelial plexus.

Neurones of a different type in the circular muscle layer send an offshoot into the skin, while another process ends on the longitu-dinal muscle (similar observations have been made by Miss MONTI in Dendrocoelum and Planaria).

HERRICK [3]) is inclined to consider this termination as a sensory muscle ending. In that case the cell would serve skin and muscle sensibility simultaneously as do certain cells found by this author and COGHILL in the central nervous system of young larvae of Amphibiae. This explanation seems very probable, since the chief offshoot of this cell, the neurite, runs centrally, into a ventral cord ganglion.

The *central nervous system* differs from the superficial plexuses in that it contains many more neurones, which in most Scolecids lie scattered in the connectives, whereas in Annelids they sur-round them. Furthermore, most of the neurites of the neurosensory cells end here. In particular the *cerebral ganglion* which is connected with the sense organs of the head (antennae, palpi, eyes and nuchal organ [4]) receives many neurites of neurosensory cells (see fig. 17).

---

[1]) DAWSON. The intramuscular cells of the earthworm. Journ. of Comp. Neurology, Vol. 32, 1920.

[2]) HESS. The nervous system of the earthworm, Lumbricus terrestris Journ. of Morphol. and Physiology. Vol. 40, 1925.

[3]) HERRICK. Neurological foundations of animal behaviour. New York, 1924.

[4]) RETZIUS believed that, in Polychaete worms, there are real sense cells in this organ in connection with bipolar ganglion cells in the central ganglion of the nuchal nerve. According to FORTUYN they are however, centrally migrated neurosensory cells ending in the nuchal organ.

Similarly the neurites of the neurosensory epithelium of the otocysts end in the oesophageal ring (ASHWORTH [1])) or in the frontal part of the ventral cord, in the caudal part of which neurosensory cells of the trunk send their neurites.
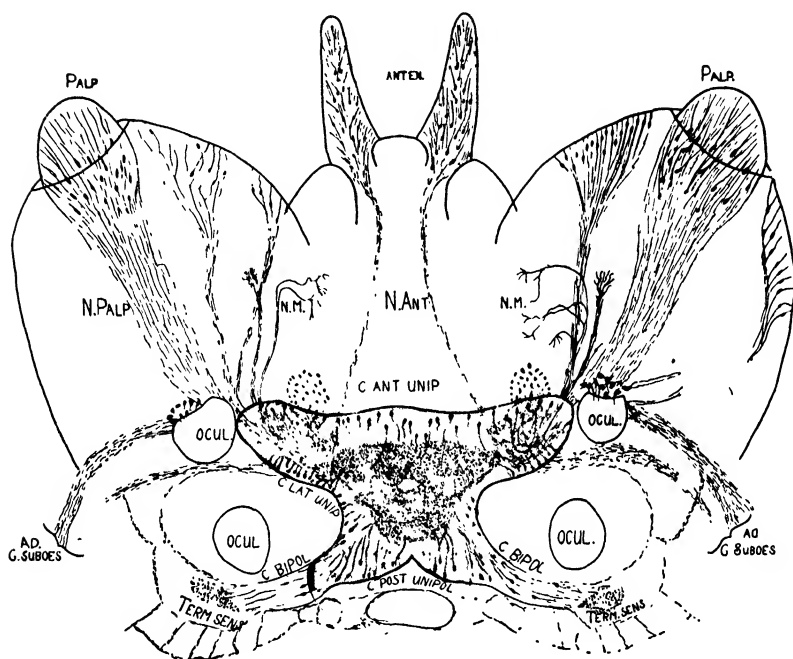
Fig. 17. Head of Nereis diversicolor, after RETZIUS. Cerebral ganglion shaded. Note the amount of neurosensensory cells in the antennae, palpi and skin.

HAVET [2]) saw those neurites in Distomum hepaticum ending, for the most part, homolaterally, though sometimes heterolaterally, while in some cases they have terminations on both sides. They

---

[1]) ASHWORTH. S. 14, B. C. Memoirs No. 11, 1904. Arenicola.

[2]) HAVET. Contribution à l'étude de système nerveux des Trematodes. La Cellule, Tome 17, 1900.

PLATE I.
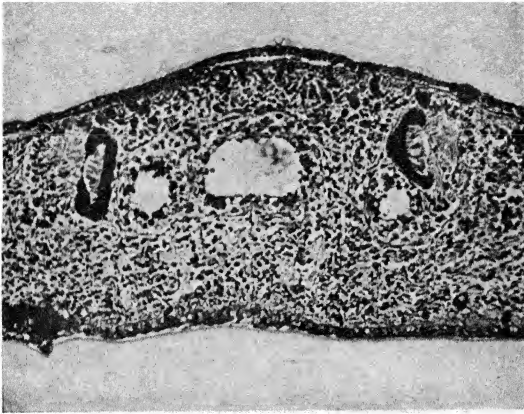
Eyes of a flatworm (Polycelis).
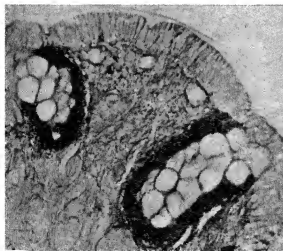
Solitary and aggregated eyes
of an Annelid Haemopis
sanguisuga.

KAPPERS.

generally give off ascending and descending branches, as has also
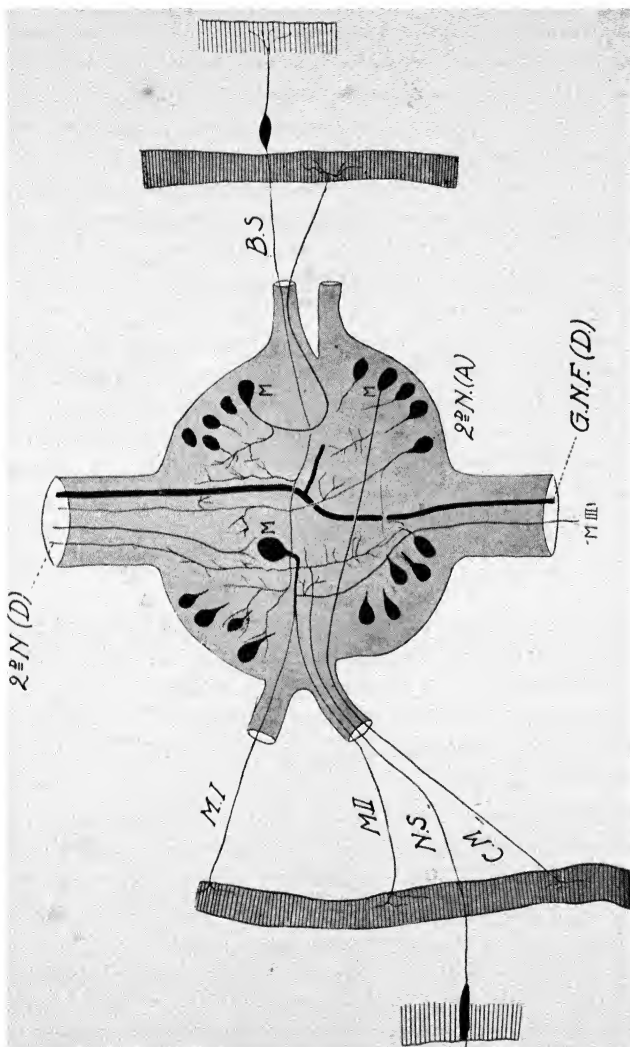
Fig. 18. Ventral cord ganglion of an Annelid: Aulastomum gulo. Composed from drawings by RETZIUS. M = Homolateral and crossing motor neurones. In the middle of the ganglion a large motor cell M (occurring in the suboesophageal ganglion) with neurites dichotomizing (MI and MII) into two roots, and another (MIII) in the connective. G.N.F.(D.) = descending giant nerve fiber with collateral; 2D N (D) descending secondary neurone; 2D N (A) = ascending secondary neurone; B.S. = peripheral sensory neurone with endings on both sides; N.S. = neurosensory cell.

been observed in Annelids (fig. 18, N.S.) by VON LENHOSSEK, RETZIUS and CERFONTAINE.

This prevalence of neurosensory cells as receptors is very interesting,

and establishes a great contrast to the vertebrates, where bipolar sensory neurones replace their function as touch receptors.

Neurites of *bipolar neurones* also enter into the headganglia and ventral cord. Their cell bodies, however, mostly remain near the skin (DEINEKA [1])) into which they send their fibrillae (APATHY; p. 58, note 1). Some of these sensory neurones have central endings on both sides of the ganglion, as the one drawn in fig. 18 (B. S.).

Only few bipolar cells of sensory neurones lie *inside* the central ganglia (HOLMGREN, GOLDSCHMIDT, DEINEKA and RETZIUS), also terminating with simple endings in the skin. DEINEKA, in particular, has described such cells in the oesophageal ring of a scolecid, Ascaris, in connection with the labial papillae.

As stated above, in the lower worms the central cells are mostly scattered between the fibers, while in the higher worms (Nemertini and Annelids, fig. 18), they lie mainly at the periphery of the ganglia and sometimes of the connectives thus surrounding the *neuropilema*.

By their peripheral arrangement these cells acquire a special form as *unipolar neurones*, having only one stem, which enters the neuropilema, and here branches into a neurite and dendrites.

The majority of the central cord cells are *motor root cells* and *secondary cells*.

Motor root cells also occur in the headganglion but they are few, serving only the movements of antennae (N. mot,, fig. 17). In the ventral cord they are more numerous.

Their fibers do not, however, always end directly in muscles, but sometimes have a praeganglionic character, ending in a peripheral intramuscular ganglion (cf. also p. 51), as is still found in the autonomic system of vertebrates (p. 85).

Direct motor cells, however, certainly occur (fig. 18). Miss MONTI saw them even in so low a form as Dendrocoelum. They generally run homolaterally but a crossed course is not rare (RETZIUS and CERFONTAINE).

In a special sort of motor cell (M), observed by RETZIUS, the neurite dichotomizes into two roots (M^1 and M^2) and a third branch (M^3) may run in the connective. Perhaps this branch leaves the cord in another segment, as occurs in crustacea (p. 58). Even in

---

[1]) DEINEKA. Das Nervensystem von Ascaris. Zeitschr. f. wiss. Zool., Bnd. 89, 1908.

larvae of amphibia, HERRICK and COGHILL found motor root fibers
of several segments arising from one cell.

GASKELL Jr. observed *chromaffin, cells* in the cord ganglia. In
addition many *secondary cells* occur, *neurones* as well as (in the
lower worms especially) *primitive ganglion cells.* Also the secondary
neurones are generally unipolar cells but multipolar and bipolar
neurones also occur among them. Most of their neurites run caudally,
subserving aboral reflexes.

In some Scolecids (Nemertini), and in most higher worms (Annel-
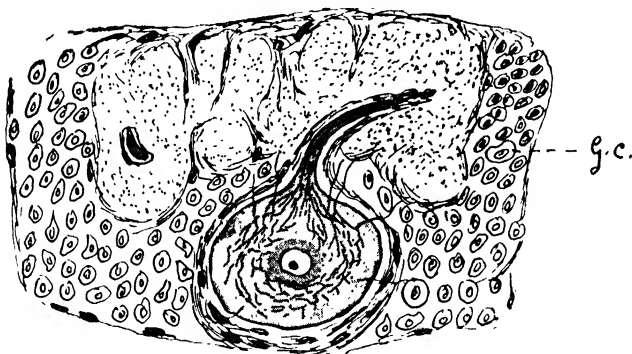
Fig. 19. The 4th giant nerve cell and its neurite in Halla par-
thenopeia, surrounded by sheath cells, (after ASHWORTH).
G.C. = ordinary ganglion cells. At the left is the neurite of the
3d giant nerve fiber. The dark zone around the nucleus contains
a great deal of basophil substance. Neurofibrillae of adjacent
tracts pass the sheath to enter the giant cell.

ids), *giant neurones* occur, giving off very large descending nerve
fibers: *neurochords.* BÜRGER [1] saw them in Cerebratulus, where they
originate from cells in the head ganglia, and from cells lying on the
periphery of the connectives, while RHODE [2] gave a complete
description of these giant fibers and cells in the polychaete Annellid
Sthenelais. They were carefully examined by ASHWORTH [3] in a

[1]) BÜRGER. Nemertini. In BRONN's Klassen und Ordnungen der Tierreichs.
Bnd. IV, Suppl. 1897—1903.

[2]) RHODE. Histologische Untersuchungen über das Nervensystem der
Polychaeten. Zool. Beitr. Bnd. 2. 1900.

[3]) ASHWORTH. The giant nerve cells and fibers of Halla parthenopeia. Philos.
Transactions of the Royal Soc. of London. Series B. Vol. 200, 1909, p. 489.

very long (1 M.) Annelid, Halla parthenopeia, and in Aglaurides.

ASHWORTH found their cells in some of the first ganglia, and smaller ones in some of the last segments. There are eight couples of such cells, each couple lying in the posterior part of the segment to which it belongs. Those of the 2d—4th segments may have a diameter of 150 micra, while others, developing later, are only 30—55 micra.

These cells, especially near the axone, contain a great many fatty granules, similar to those in the surrounding smaller cells (mitochondria?). Basophil tigroid granules also occur, especially around the nucleus and apparently arising from it. Most of the neurofibrillae lie peripherally to this perinuclear tigroid (fig. 19). They continue in the axon.

The axon decussates and then runs backward. It is surrounded by myeline (HIRSCH) and by sheath cells. Whereas the giant fibers of Halla and Aglaurides are single, those of Arenicola, Axiothea, Clymene and Lumbricus are collected from different giant cells into a compound axon [1]), as is also observed by VAN DER HORST in Mauthner's fibre of Ceratodus, and by HERINGA in peripheral nerves.

The neurochords of the frontal giant cells end in the caudal neuropilema, but they give off collaterals to motor root cells of the segments through which they pass (fig. 18). According to CERFONTAINE, GAMBLE and ASHWORTH, some of the collaterals even enter the motor roots themselves (cf. page 35).

The question remains open whether such collaterals terminate directly on muscle tissue or on peripheral motor ganglion cells lying in the muscle tissue. The giant ganglion cells of the caudal segments are much smaller (25—30 micra). Their axons, also decussating in Halla, run to the anterior segment.   .

The neurochords only influence the longitudinal muscles, producing a sudden shortening of the body, thus subserving a rapid reflex.

They functionally resemble the giant nerve fibers of Amphioxus (fig. 40).

A great many smaller secondary neurones, homo- as well as contralateral, occur in Annelids. Most of these also descend. This is

---

[1]) BROWN (Journ. of Comp. Neur., 1927), supposes this fiber to be segmented. As local sheath cells may participate in the formation of fibrils (APATHY, HELD, BOEKE, HERINGA) this may explain its segmented character.

not so strange, since most sensory impulses in invertebrates are elaborated by aboral reflexes (as also in lower vertebrates). These shorter neurones — running from segment to segment — may cause the slow undulating segmental movements innervating motor root cells of the circular muscle (HERRICK l. c.).

In addition large ascending neurones occur, carrying body stimuli to the brain ganglion to be correlated with head impulses. They are much less numerous than the descending ones, and the great development of the cerebral ganglion in these animals depends chiefly on its direct connections with the sense organs of the head (fig. 17), particularly with the neurites of the neurosensory cells as mentioned above (p. 33).

In other words, the cephalisation in worms is mainly a *primary* one depending on the large size and number of sense organs in the headregion and on some motor nerve fibers for adjacent musculature including sympathetic fibers [1]) for the intestina.

Associative cephalisation, only occurs in the highest form of Annelids (Polychaeta), where *corpora pedunculata* (HALLER [2]) or globuli (HOLMGREN [3]) are found.

The latter are groups of small, unipolar cells arranged like a mushroom on the top of a stalk (peduncle). These *mushroom bodies* are centers for correlation, whose development in these animals largely depends on the eyes and palpi (HANSTRÖM). They seem to occur first in Eunice, and are largest in Sthenelaïs [4]).

We do, not however, know if the head ganglia in higher Annelids have, among other functions, an inhibitory influence on lower centres, as has been proved to exist in Molluscs (Aplysia) and insects (Aeschna), and which is so characteristic of the forebrain of mammals. So far nothing has been observed in favor of such an inhibitory influence of the head ganglion in worms.

---

[1]) In some higher Annelids sympathetic fibers for the caudal intestinum arise from the posterior cord ganglion (PLATE, cf. page 83).

[2]) HALLER. Beiträge zur Kenntnis der Textur des Zentralnervensystems der höheren Würmer. Arb. a. d. Zool. Institut der Universität Wien, Bnd. 3, 1889.

[3]) HOLMGREN. Zur vergleichenden Anatomie des Gehirns von Polychäten etc. Kungl. Svenska Vetenskaps Akademiens Handlingars, Bnd. 56, 1916.

[4]) HANSTRÖM. Das zentrale und periphere Nervensystem des Kopflappens einiger Polychaeten. Zeitschr. f. Morph. und Ökologie der Tiere. Bnd. 7, Heft 7, 1927.

Molluscs.

In Molluscs also, we may distinguish a superficial plexus and a deeper, more concentrated nervous system.

In the most primitive Molluscs, *Amphineura*, the *superficial plexus* resembles that of Coelenterates.

So the subradular organ of Chitons (HALLER [1])) contains a ganglionic *fiber plexus*, consisting of *primitive ganglion cells* and neurites of *neurosensory cells*.
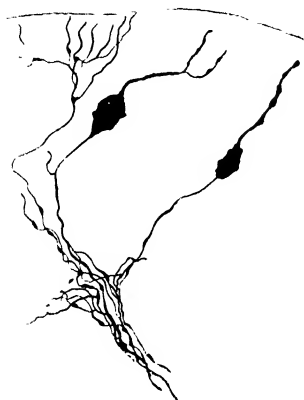
Fig. 18. Sensory free endings in the epithelium of Limax and neurosensory cells with one and two peripheral offshoots, thus resembling bipolar neurones. VERATTI.

But also the higher Molluscs: snails, shellfish and cuttlefish have peripheral plexuses, specially in the foot (EDINGER [2]), and arms, (p. 50, 51). These plexuses have a great deal of functional independence. Thus Limax may go on crawling after the removal of its central ganglia. But these plexusses are different from those in Coelenterates and Chiton, as they not only contain primitive ganglion cells and neurites of neurosensory cells but also bipolar neurones, and their network does not only consist of *single* fibers, but contains also *bundles* (BIEDERMANN [3]). FORTUYN calls this a *nerve plexus* (instead of a *fiber* plexus).

A remarkable part of the peripheral subepidermal plexus in Molluscs is that connected with the *osphradium*, a sense organ near the gills, probably serving for testing respiration water. It occurs only in water living molluscs and consists of neurosensory cells

---

[1]) HALLER. Die Organisation der Chitonen der Adria. Arb. aus dem Zool. Institute der Univ. Wien, Bnd. 4 & 5, 1882, 1884.

[2]) EDINGER. Die Endigung der Hautnerven bei Pterotrachea. Arch. f. mikrosk. Anatomie. Bnd. 14, 1877.

[3]) BIEDERMANN, Die Innervation der Schneckensohle. Pflüger's Archiv Bnd 111, 1906.

which terminate in a ganglion lying directly underneath the epithelium of the osphradium (GILCHRIST [1]).

An interesting fact is that among the bipolar neurones of the subepidermal plexus there are many transitional stages of neurosensory cells (fig. 20).

As HAVET did in worms, VERATTI [2]) observed in Molluscs neurosensory cells with two or more receptive offshoots (especially in the tentacles). These offshoots, moreover, may be fairly long so that the cells acquire a close resemblance to bipolar neurones.

VERATTI could not always distinguish sensory neurones freely ending in the skin from neurosensory cells with branching peripheral offshoots, a strong argument indeed for the conception that bipolar sensory neurones arise from. or, at least, are closely related to neurosensory cells.

As already mentioned (p. 14) in the tentacles of Helix pomatia, neurosensory cells occur whose neurites end immediately in the tentacular muscle (SAMASSA [3])), thus allowing
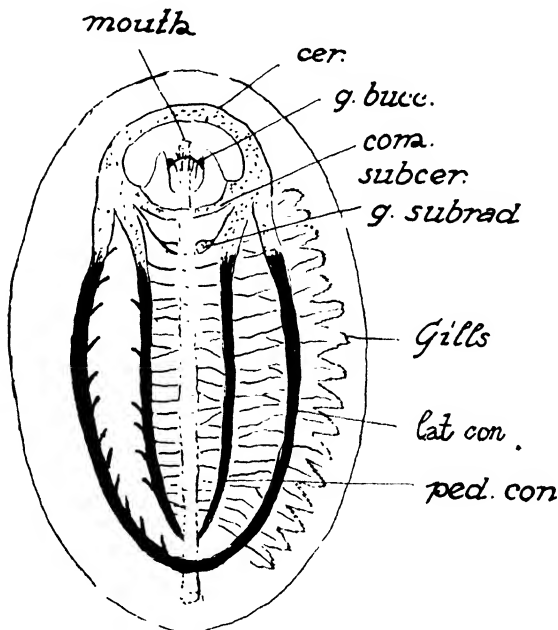
Fig. 21. Scheme of the central nervous system of Chiton, (after PLATE). The transverse inter pedal connections are real commissures, those of the lateral connective only extend to the pedal connective of the same side.

___

[1]) l. c. infra.

[2]) VERATTI. Recherche sul sistema nervoso del Limax. Memorie del R. Inst. Lombardo, Vol. 18, 1900.

[3]) SAMASSA. Ueber die Nerven des Augentragenden Fühlers von Helix pomatia. Zool. Jahrb. Abtheil. f. Anat. & Ont. Bnd. VII, 1893.
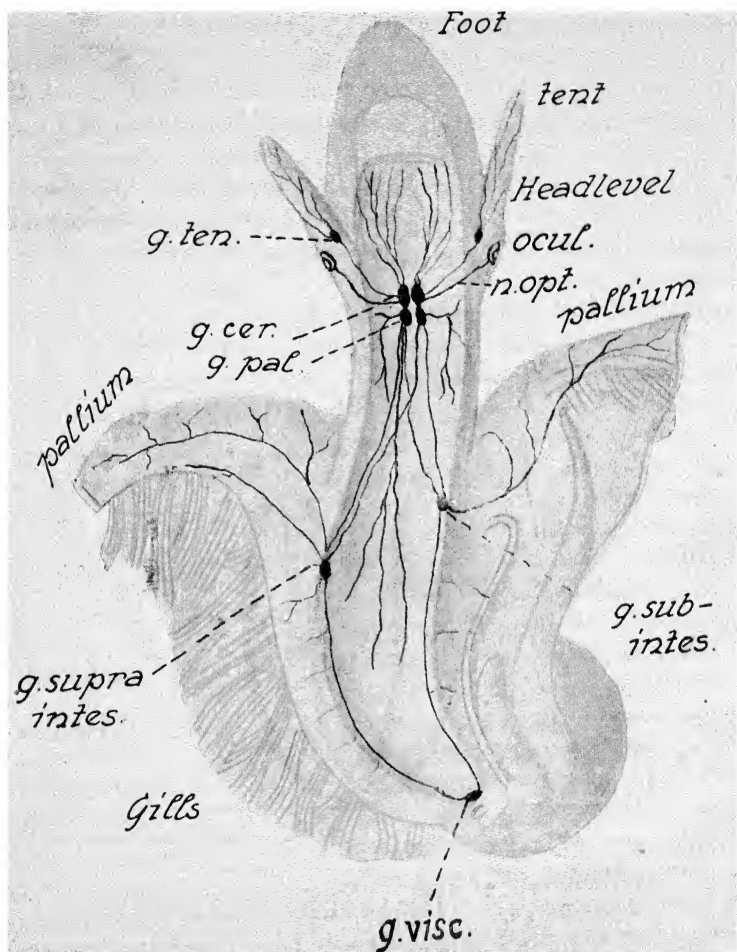
Fig. 22. Xenophorus after Bouvier [1]). Nervous system in situ.
Head largely removed. The pedal ganglia lie in the foot under-
neath the cerebral ganglion. For the chiastoneury of the pleuro-
(= pallio-) intestinal nerves s. p. 43.

[1]) Bouvier. Morphologie générale et classification des Gastéropodes proso-
branches, Thèse Paris. 1887. In the Prosobranch Littorina and Neptunca
(also in the Pulmonate Limnaea) the peripheral tentacular ganglion fails, the
tentacula being directly innervated from the cerebral ganglion (Hanström:
Innervation der Fühlern bei stylommatophoren and basommotophoren
Pulmonaten: Zool. Anz. Bnd 66, 1926 (see also Acta Zool. Bnd 6 1925).

for a very quick reflex, and showing at the same time that neurosensory cells, in addition to receptive and conductive properties, may also have an effective function.

The *central nervous system* of most molluscs is very different from that of worms.

In primitive forms, the *Amphineura* (fig. 21), it still consists of a circumoesophageal ring and two pairs of longitudinal ganglionic strings, still very near the epidermis, the lateral representing the
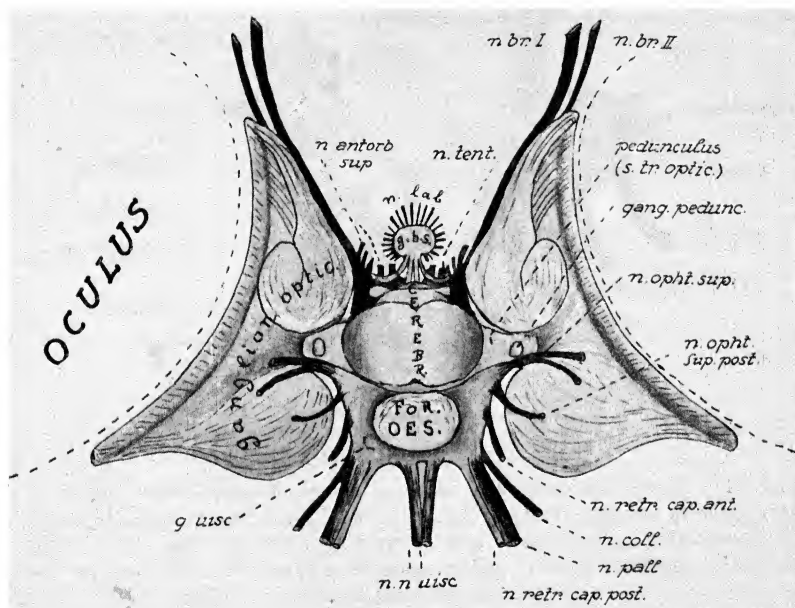
Fig. 23. Dorsal aspect of the brain and adjacent optic, visceral and superior buccal (g.b.s.) ganglia of Sepia officinalis after HILLIG. The pedal and brachial ganglia (fig. 24) are invisible, lying underneath the cerebral.

pleuro-visceral, the medial the pedal connective of higher Molluscs.

Transverse commissures between the pedal strings are present, though irregular. This primitive arrangement however, only occurs in *Amphineura* (*Chitons* as well as *Solenogastres*). It disappears in higher Molluscs. Even in the symmetrical (euthyneur [1]) Lamelli-

---

[1] Euthyneur is the contrary of chiastoneur (see p. 43). It means that the nervous system is direct (not crossed).

branchiata and Cephalopods, the commissures are generally lacking (except the circumoesophageal ones). They remain in few Gastropods only, mainly between the two strings in the pedal region. These
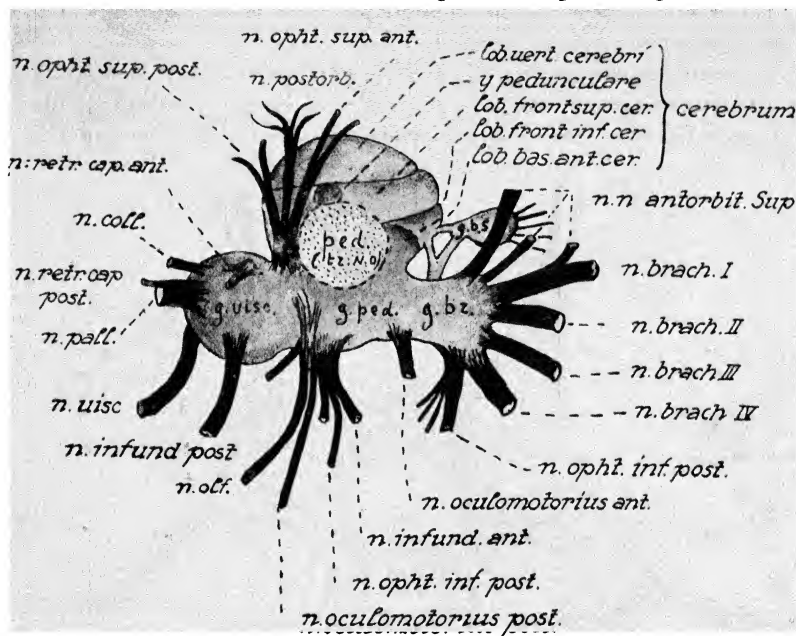
Fig. 24. Lateral aspect of the brain of Sepia officinalis after HILLIG [1]). The optic ganglia are removed by a section through their peduncle (ped.) The brachial ganglion (g.br.) and visceral ganglion (g. visc) have joined the pedal ganglion (g.ped.) which again is immediately attached to the cerebral ganglion.

strings may be the homologues of the ventral strings of Turbellaria, and, with their retention of commissural connections, remind us of the rope ladder system (f.i. Photinula, PLATE). In most Gastropods, (see fig. 22), in Lamellibranchiate and Cephalopods there is no indication whatever of a rope ladder system.

A special sort of concentration takes place in higher Molluscs, the ganglia of the ventral or pedal strings here grouping into one

[1]) Das Nervensystem van Sepia offinicalis, Zeitschr. f. Wiss. Zool. Bnd. 101, 1912.

pair of *pedal ganglia,* and those of the lateral strings into the *pleurovisceral ganglia* [1]). These two pairs of ganglia, moreover, show a tendency to comglomerate with the *cerebral ganglia.* The three sets of ganglia, which, in Lamellibranchiata and in lower Gastropods, such as Paludina, still lie some distance away from each other approach one another more and more closely (c.f. v. JHERINGS splendid monography [2])).

Thus GILCHRIST [3]) found in Pleurobranchus, and DAKIN [4]) in Buccinum, a very compact relationship of these ganglia (for Xenophorus see fig. 22).

The twisting of the body in most Gastropods gives rise to a loss of symmetry in the nervous system. A peculiar decussation of the connectives — CHIAS-TONEURY — is a consequence of it. This consists of a crossing of the pleuro intestinal connectives so that the pleural (= pallial) ganglion of one side is connected with the intestinal of the other side (see fig. 22). However, in addition to this decussation a secondarily acquired homolateral connection occurs.

The greatest concentration takes place in Cephalopods [5]), where the cerebral, pedal and visceral ganglia form practically one mass (see fig. 23 and 24) to which the brachial ganglion is added.

The histological structure of the *central nervous* system in the *Amphineura* is still primitive, the cells in the cord- and brain ganglia being scattered among the nerve fibers, as in flatworms. In the higher Molluscs (fig. 25) they are arranged peripherally to the neuropilema as in Annelids. Neurites of the pilema envelop these cells with basketlike telodendria (fig. 25c).

The head ganglia receive a large number of neurites from the neurosensory cells of the tentacles, eyes, and statocysts [6]). In

[1]) The pleurovisceral ganglia may be represented by different groups, such as the pleural (pallial) the visceral, and the supra- and subintestinal ganglia.

[2]) v. JHERING. Vergleichende Anatomie des Nervensystems und Phylogenie der Mollusken: Engelmann, Leipzig, 1877.

[3]) GILLCHRIST. Notes on the minute structure of the nervous system of the Molluscs. Journ. of Linnean, Society Zoology, Vol. 26, 1898, p. 179.

[4]) DAKIN. L. M. B. C. Mémoirs No. 20, Buccinum. Williams and Norgate, London, 1912.

[5]) For the different degrees of concentration in Inkfishes see PFEFFERKORN. Das Nervensystem der Octopoden. Zeitschr. f. Wissensch. Zoologie, Bnd. 114, 1915.

[6]) Chiton has no statocyst. In the other Molluscs it is nearly always present but its innervation varies. Originally the N. staticus is connected with
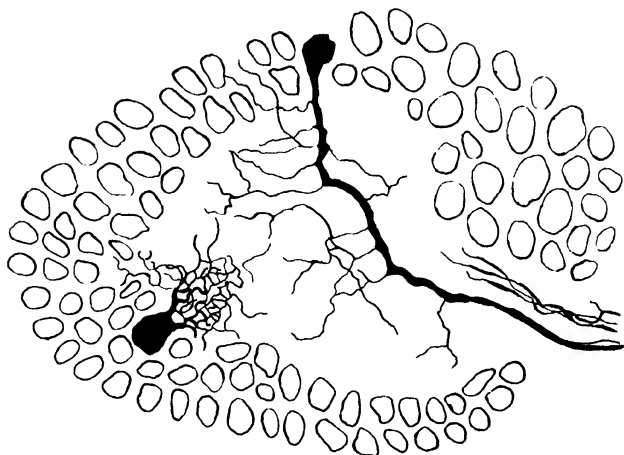
Fig. 25a. Section of a pedal ganglion in Limax. Dorsally a cell of the first type. Ventrally a cell of the second type. VERATTI.
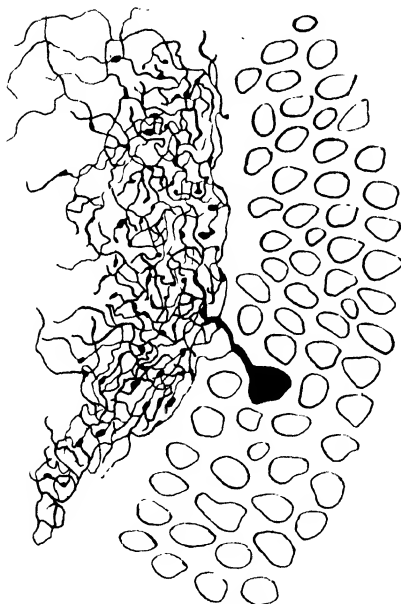
Fig. 25b. Section of a part of the cerebral ganglion in Limax with a cell of the second type. VERATTI.
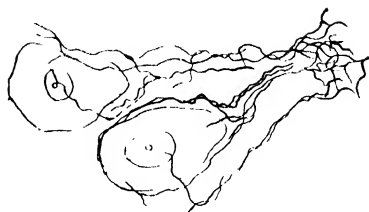
Fig. 25c. Interneuronal connections in Limax.

Pulmonates (see also Xenophorus, fig. 22) those of the eyes and statocysts terminate closely to one another, thus showing the close relationship between these two organs of orientation.

An interesting fact was observed by *Tschachotin* [1]) in Pterotrachea, where the nerves of the highly developed static organs of both sides form a semidecussation, a *static chiasm*, resembling the optic chiasm of mammals. This semidecussation apparently is a consequence of the simultaneous collaboration of the lateral half of one statocyst with the medial half of the other, since it is evident that when the animal turns over one side the statolith stimulates the lateral side in one cyst while it stimulates the medial side in the other. This arrangement is a striking example of *neurobiotaxis* in neurites of neurosensory cells, especially of the phenomenon (also observed in the junction of the ventral connectives in Annelids) that simultaneously stimulated nerves tend to join. The semidecussation of the optic nerve in the higher mammals falls under the same law.

The statocysts influence the tonus (MUSKENS), also of the eye-muscles [2]).

Olfaction in Molluscs is located on rhinophores or on tentacles, that are provided with neurosensory epithelium closely resembling the olfactory epithelium in vertebrates (RETZIUS [3]).

The *motor root cells* in the central nervous system show relations similar to those of Annelids, being unipolar.

the brain ganglion, as e.g. occurs in Gastropods. In Lamellibranchiate various relations are seen. In some the nerve still enters the brain ganglion (Pecten, Lima). In others (Anodonta) it enters the cerebro-pedal connective, but in Mya, Venus and some others, it enters the pedal ganglion. The same migration of its emergence is seen in cuttlefish, where it enters the brain ganglion in Nautilus, and the pedal ganglion in Octopus.

This migration is due, according to PLATE, whom I quote, to a migration of the statocyst itself from the head region to the footregion. It would be interesting to know if in those animals where the nerve root enters the pedal ganglion, its fibers do not run inside the cerebro-pedal connective to the brain ganglion, since we know from vertebrate neurology that the apparent entrance of a nerve may change without, however, changing its central connection.

[1]) TSCHACHOTIN. Zeitschr. f. wissensch. Zool. Bnd. 90, 1908. Die Statocyste der Heteropoden.

[2]) From the static nerve a branch runs directly to an eye muscle nerve so that here, as in the tentacles, a direct neurosensory-motor innervation may occur.

[3]) RETZIUS, Biologische Forschungen. N. F. Bnd IV, and IX, 1892, 1900.
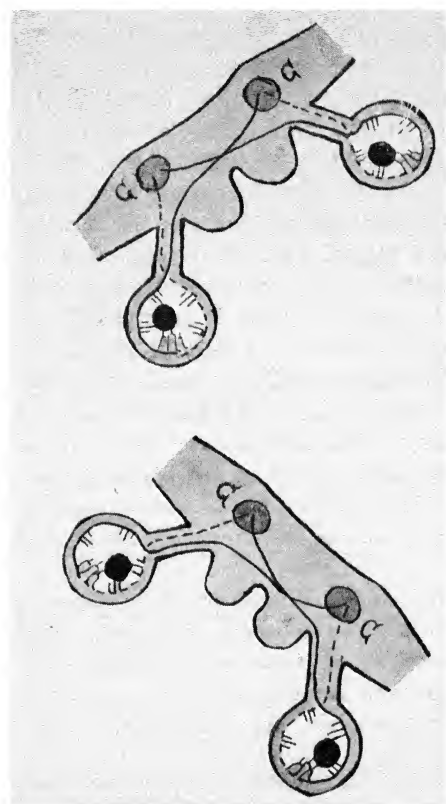
Fig. 26. Semidecussation of the statocyst fibres in Pterotrachea by which the simultaneously stimulated outer half of one and inner half of the other statocyst are projected in the same ganglion (G). Fibers of the inner halves dotted, of the outer halves full.

The *secondary neurones* are represented by unipolar cells of the 1st type of GOLGI (having long neurites), and by 2d type cells having neurite that branches near its origin. The neurite of the first sort (fig. 25a) runs to other ganglia, while the latter (fig. 25b) establishes many intraganglionic connections (VERATTI).

GILCHRIST (l. c.) found that these cells are tinctorially different

towards methylene blue. When the cells of one type are stained, the others are not, and vice versa.

Among the descending secondary neurones, the so called "pyramidal tract" in Pulmonates is important, arising near the static and optic centres, and running to lower ganglia through the cerebro-pedal connectives (partly crossing).

The concentrated nervous system, which, at the same time, is the most highly developed is that of the *Cephalopods* (cf. fig. 23, 24, 27). Especially the visual system of these animals is frequently studied. Already in Lamellibranchiates and Gastropods this system is highly developed (for their eyes, see plate II). The eye of Cephalopods (except Nautilus, which, in this respect, resembles the Prosobranch Haliotis) in even compared to the vertebrate eye [1].

The visual chain in Cephalopods, however, differs (v. LENHOSSEK [2], KOPSCH [3]) from those in vertebrates, since the cephalopod retina contains only the light percipient neurosensory cells, the other retina cells of vertebrates lying in the optic lobe of the brain ganglion (fig. 27).

As, however, in vertebrates the whole retina arises from the brain vesicle, this difference is not so significant, the secondary and tertiary neurones in the vertebrate retina being originally also cells of the central nervous system.

The chief difference is, that the eye and the brain ganglion in Cephalopods originate separately from the ectoderm, while their ectodermal primordia in vertebrates are fused from the beginning, thus establishing, ab origine, a connection which, in Cephalopods, is acquired secondarily.

The long neurites (A) of the light percipient cells of cuttle fish, running to the cortex lobi optici, form a chiasm so that the image on the retina (being reversed by the narrow pupil and the lens) is reversed again, thus practically corrected in the cortex lobi optici (CAJAL). Some of them end under the cortex (KOPSCH [4]).

In this cortex two cellular strata, an *outer* and an *inner granular*

---

[1] See GLOCKAUER, Zur Anatomie und Histologie des Cephalopodenauges. Zeitschr. f. wiss. Zool., Bnd. **113, 1915**.

[2] VON LENHOSSEK. Zur Kenntnis der Netzhaut der Cephalopoden. Zeitschr. f. wiss. Zool. Bnd. 58 1894 and Histologische Untersuchungen am Sehlappen der Cephalopoden. Arch. f. mikr. Anat. Bnd. **47, 1896**.

[3] KOPSCH. Das Augenganglion der Cephalopoden. Anat. Anzeiger, 1895.

[4] On the basal offshoots of (amacrine) cells of the outer granular layer.

layer, occur, separated by a thick plexiform layer. Both *granular layers* contain *amacrine* cells, the offshoots of which end under the respective layer.

These are primitive ganglion cells, the unspecialized offshoots of which are in contact with the telodendria of visual and efferent fibers (see fig 27).

CAJAL [1]) supposes that these cells, (which have no neurites [2]), store nervous energy, which is discharged when impulses of the afferent visual path run along their offshoots, thus adding to the strength of their effect on the bipolar cells.

Thus these cells (which also occur in the eyes of vertebrates) may serve for summation of stimuli and integrate the discharges of the visual neurites on the bipolar cells.

Underneath the outer granular layer, in the *plexiform or fiber layer*, most of the neurosensory neurites (A) end upon dendrites of bipolar cells, which lie in the *inner granular layer* (KOPSCH) [3]).

The structural similarity of this system with the retina of vertebrates is still completed by the fact that in the plexiform layer neurites of large *horizontal cells* are found, similar to those of the vertebrate retina, and apparently coordinating different regions. These long neurites run in the plexiform layer, but originate in large cells of the inner granular layer (not drawn in fig. 27).

The bipolar cells (cells of LENHOSSEK) are intercalated neurones (B) between the neurosensory neurites and the tertiary optic cells, whose neurites (C), corresponding serially to our optic nerve, form the (uncrossed) *peduncle* and end upon cells of the *optic ganglion* (D).

From this *optic ganglion* a new tract runs, partly directly (D[1]), partly decussating (D[2]), to the *peduncular ganglia* (E).

These ganglia develop later than the optic lobe or retinal ganglion, but are not homologous to the corpora pedunculata (or globuli) of Annelids and Arthropods, which are supposed to occur among Molluscs in Gastropods only (HALLER [4]).

---

[1]) RAMON Y CAJAL. Contribucion al conocimiento de la retina y centros opticos de los cefalopodos. Trabajos del laboratorio de Investigaciones biologicas de Madrid. Vol. XV, 1917.

[2]) This is why they are called "amacrine" (i. e. having no long — macron — offshoot).

[3]) According to CAJAL most of these cell bodies lie in the outer granular layer, the inner granular layer also containing chiefly amacrine cells.

[4]) HALLER, Die Intelligenzsphären des Molluskengehirns. Archiv f. mikr. Anatomie, Bnd 81, 1913.

PLATE II.
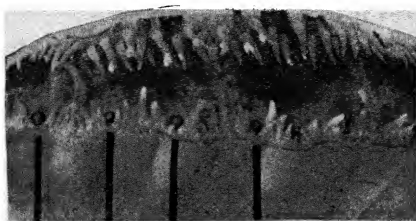
Lens eyes of Pecten opercularis.

cornea

lens

N. opt.

neuro-epith.

N. opt.
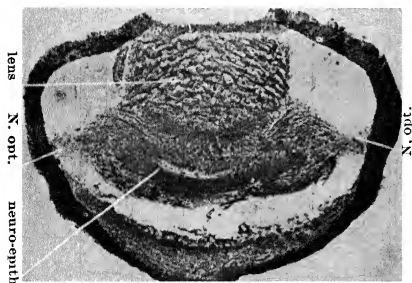
Lens eye of Pecten opercularis.

cornea

lens

neuro-epith.
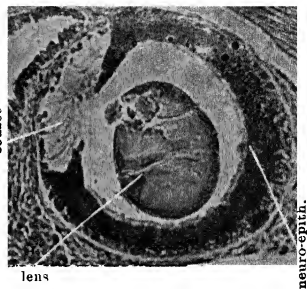
Lens eye of Helix pomatia.
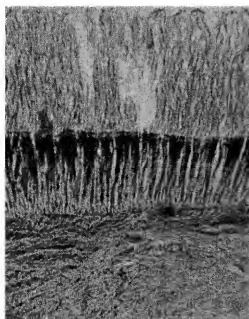
Retina of the camera eye
of Nautilus.
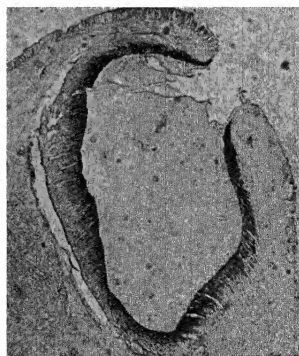
Camera eye of Haliotis.
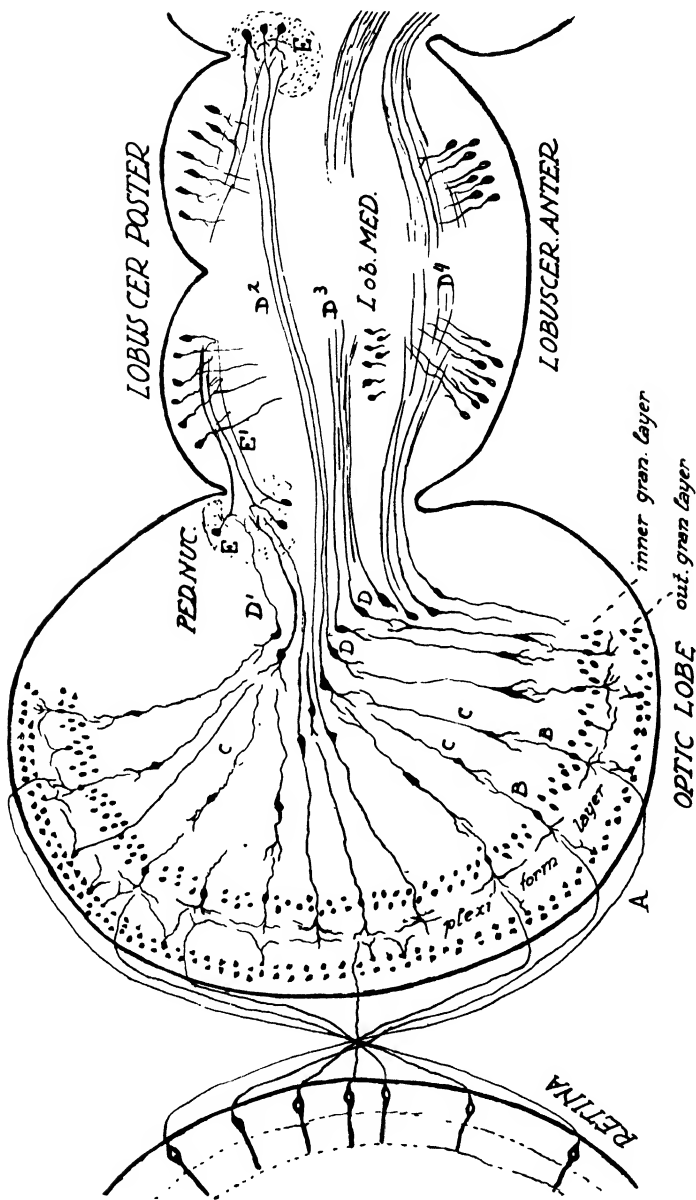
Fig. 27. Scheme of the visual paths and their central connections in a cephalopod, combined from VON LENHOSSEK, KOPSCH and (chiefly) CAJAL. — According to CAJAL most bipolar cells (B) are located in the outer granular layer.

Other reflectory tracts (D^3, D^4) run from the optic ganglion to the anterior and median lobes of the "cerebrum", while the posterior lobe receives fibers from the peduncular ganglia (by E^1).

I have entered into these details somewhat more than the scope of this survey might permit, because these relations show that, however high the organisation of the nervous system in these molluscs may be, the optic system exhibits an incomplete concentration in comparison with vertebrates where the whole visual apparatus including the neurosensory epithelium, is concentrated in a part of the brain vesicle.

A similar lack of concentration occurs in the *locomotor system* of these animals, whose innervation does not depend only upon motor cells of central ganglia, as it does in Vertebrates, but chiefly on local ganglia, situated near or even between the muscles, as is illustrated in the arms of Octopus (Guérin) [1].

Each arm has an axial strand of neuropilema surrounded by unipolar cells on three sides, the fourth side being covered by two longitudinal fibre tracts.

These longitudinal fibre tracts are connected with the brachial ganglion of the central nervous system (see fig. 24, Sepia). Guérin [1] supposes one tract to be centrifugal and the other centripetal.

This axial nervous complex is surrounded by the brachial muscle, strips of which run to the muscles of the adhesive discs. In the brachial muscle and between this and the disc muscles, small peripheral ganglia lie, the neurites of which, together with those of the axial cells, innervate the brachial muscles. Ascending sensory fibers run to the cerebrum. Consequently these muscles are not innervated *directly* by the brachial ganglion of the central nervous mass, but by *local peripheral ganglia*. The same arrangement is seen in the mantle musculature, which is innervated by the stellar ganglion (v. Uexküll [2]), Baglioni [3]),

---

[1]) Guérin. Contribution à l'étude des systèmes cutané, musculaire et nerveux de l'appareil tentaculaire des Céphalopodes. Arch. de Zoologie experimentale. 4 Serie Tome 8, 1908. See also Droogleever Fortuyn (l.c.).

[2]) v. Uexküll. Physiologische Untersuchungen an Eledone moschata. Zeitschr. f. Biologie, Bnd. 28, 1891.

[3]) Baglioni. Physiologische Differenzierung verschiedener Mechanismen des Zentral nervensystems. II Untersuchungen an Eledone moschata und anderen Wirbellosen. Zeitschr. f. allgem. Physiol. Bnd. 5, 1905,

BOZLER [1]), which ganglion also receives impulses from a central ganglion. A simular *innervation* occurs in the *autonomic* or *sympathetic system* of octopods, which arises from the buccal ganglia.

As we shall see (p. 84) the autonomic innervation of Vertebrates is also established by peripheral ganglia which are again connected with the central nervous system. Consequently the mantle and brachial ganglia of Cephalopods may be compared to the postganglionic sympathetic ganglia of vertebrates. This is also interesting in connection with the fact that the locomotor musculature of Cephalopods is unstriped musculature.

Though the chainlike arrangement of superimposed motor cellgroups also occurs in the autonomic system of vertebrates there would be a difference between the loco-motor organisation of Cephalopods and that found in the sympathetic system of vertebrates, if FRÖHLICH's statement [2]) were true, that the stellar gangilon receives neurites of sensory cells in the skin, since the sympathetic postganglionic ganglia do not receive sensory fibers or only very few.

Nearly all the sensory fibers of the vertebrate sympathetic system run directly to the spinal cord. Sensory endings in local autonomic ganglia are described by MICHAILOW, and by E. MÜLLER, but doubted by most other authors. Most reflexes that occur here, are certainly axon reflexes, mediated by cellulopetal impulses from the telodendria of motor cells, spreading over collaterals.

These peripheral locomotor ganglia are another illustration of the fact that the nervous system of Cephalopods, however highly developed in many respects, is not concentrated to such an extent as the vertebrate central nervous system, and thus show for the motor system the same as is shown for the sensory system by the eye.

Arthropods.

Just as the nervous system of primitive Molluscs (Chitons) resembles that of flatworms so the arrangement in primitive Arthropods (fig. 28 A) reminds us of the structure in lower Annelids (fig. 14).

---

[1]) BOZLER. Ueber die Funktion des Stellarganglions der Cephalopoden. Zeitschr. f. vergleich. Physiologie, Bnd. 5, 1927.

[2]) FRÖHLICH. Das Mantelganglion der Cephalopoden als Reflexorgan. Zeitschr. f. allgem. Physiologie, Bnd. 10, 1910.

While the segmented character of the nervous system is obvious in both, also its further development shows a resemblance, the ventral connectives remaining separated in the lower forms and

LIMNADIA

Fig. 28 A. Rope ladder nervous system of a lower crustacean: the Phyllopod Limnadia (after GIESBRECHT).

APIS

Fig. 28 B. Apis mellifica after BLANCHARD. The ventral connectives are consolidated in one string. The first thoracic ganglion is still isolated, while the two others are consolidated into one. Five separate abdominal ganglia.

CONOPS

Fig. 28 C. Conops rufipes after KÜNCKEL D'HERCULAIS. All thoracic ganglia, together with some frontal abdominal ganglia are concentrated into a single mass. Similarly the caudal abdominal ganglia form one ganglion.

SARCOPHAGA

Fig. 28 D. Sarcophaga carnaria after LANG. All the thoracic and abdominal ganglia are consolidated into one ganglion.

Fig. 29. Different concentration of the frontal ganglia in two Crustaceans and an Insect after PLATE.

S.N. = sympathetic nerve arising from the tritocerebrum and from paraoesophageal ganglia (cf. fig. 46),

joining in the higher (see fig. 28). In arthropods, however, the concentration in the ventral cord goes further than in Annelids and appears in still another way.

While in some arthropods a great number of nearly equally large ganglia are distributed over the whole length of the ventral cord, in crabs, spiders and most insects these cell groups tend to collect in a postero-anterior direction. This may be shown by comparing larval and adult individuals of the same species as well as adults of different species.

Fig. 30. Maxillary palp with two sense organs connected with bipolar neurones[2]) in Palaemon, after E. HOLMGREN. The cells with dark nuclei are supposed to be ganglion cells, those with light nuclei connective tissue cells.

The final concentration in the *thoracic region* is a result of the predominance of this region in loco-motor function (*wings* and *feet* centers), and so may be explained by *neurobiotaxis*, being another example of the general law that a region from which the majority of stimuli proceeds, determines the location of the nervous centers [1]).

A similar tendency to concentration is seen in the head region of these animals, and establishes a difference from Annelids. The *cerebrum* of Arthropods is generally divided (fig. 29) into a *protocerebrum* (I), *deuterocerebrum* (II) and *tritocerebrum* (III), but it is probable that only the protocerebrum

----

[1]) In vertebrates a classic example of this phenomenon is given by the approach and final junction of the trochlear nucleus to the oculomotor nucleus, tho latter being the chief motor center of the eye (cf. fig. 66).

[2]) E. HOLMGREN himself was more inclined to consider these as neurosensory cells.

is homologous with the cerebrum of Annelids, and that the deutero-
and tritocerebrum originally were postoral parts belonging to the
ventral cord ganglia. This is most evident for the tritocerebrum,
whose ganglia in several entomostracs [1]) (see the Phyllopod in
fig. 29) still lie entirely behind the oral duct. Even in higher
crustacea and insects the commissure of the tritocerebrum still
runs behind this duct (fig. 29).

The commissures of the deuterocerebrum and protocerebrum
are imbedded in the substance of the brain. The commissure
between the deuterocerebra (c. fig. 32; c. o. fig. 33) is an ol-
factory commissure as the first antennal nerve, which ends here,
carries olfactory impulses. The commissure of the protocerebrum is
chiefly concerned with optic functions (n. o. fig. 32; com. fig. 33).

The protocerebrum of all arthropods contains in its midst a center
of importance, a special neuropilema, the *corpus centrale* (c. b.
fig. 32, c. c. fig. 33). Decapods, spiders and insects, moreover,
have the so called "pons" (fig. 33; protocerebral bridge: fig. 32),
a visual correlation centre. Besides, in most arthropods (even in
several crustacea) the protocerebrum contains corpora pedunculata
(fig. 32 and 33).

For the hodological relations in the arthropod brain I refer to
page 62. I shall first deal with the histological constituents of the
superficial nervous system.

In addition to the primitive form of sensory innervation by
neurosensory cells, still numerous in arthropods, a new feature,
perhaps first occurring here, is seen in the innervation of special
sense organs of the skin by bipolar sensory neurones [2]), the end
fibrillae of which enter *specialized epithelial cells*, forming organs of
touch. The peculiarity of this relationship is that ectodermal cells
acquire a special function as *sense cells* by the fact that they *only*
serve sensation.

While in the lower invertebrates we find sensory neurones
entering the ordinary epithelium of the skin, the above mentioned
connection is a new principle, since the primitive endings
usually lie in or against ordinary epithelial cells which retain

---

[1]) The same holds good for Arachnoïds.
[2]) I follow here the opinion of DROOGLEEVER FORTUIJN.

their epithelial covering function and have no exclusive receptive character.

Sense cells, however, are specialized epithelial cells which have but one function: the *perception* of *stimuli*. They occur in crustucea as well as in insects. In the latter they are described by GERMER [1]) among others.

Such *sense cells* introduce a new step [2]) in the evolution of the nervous system, their evolutionary significance being also demonstrated by the fact that they are more frequent in vertebrates, where they are characteristic constituents of the taste buds, lateral line organs and labyrinth, and where they acquire a special importance in the complicated sense corpuscles of the skin (corpuscles of GRANDRY, MEISSNER, etc.).

These *sense cells* are not nerve cells as they do not serve for con-duction, no neurite growing out of them, but they are of great importance for perception, as they are more fit for this function than are ordinary epithelial cells, and probably *lower the threshold of perception*, allowing finer or *eucritic perceptions* (PARSONS [3]).

The bipolar cells which innervate these cells in arthropods are generally, though not always, located very near them under the skin (fig. 30). Their neurites run to the cerebral ganglia.

Sensory cells are not the only constituents of the subepithelial plexus. Also peripheral effector cells occur in it.

Even such simple ganglionic plexuses as are found in coelen-terates, worms and molluscs are observed (E. HOLMGREN [4]),

---

[1]) GERMER. Untersuchungen über den Bau und die Lebensweise der Lymexy-loniden etc. Zeitschr. f. Wissenschaftliche Zool. Bnd. 101, 1912 (Taf. XXX, fig. 2).

[2]) RETZIUS supposed that such sense cells already occur in the nuchal organ of polychaete worms (see, however, note 1, p. 33).

The question also may arise, whether the basiepithelial ganglion cells, which, in Coelenterates, send their peripheral offshoot to the cnidocil vesicle, and whose deeper offshoots end in muscle plates, are not simpler predecessors of this sort of arrangement. I dare not answer this question in the affir-mative, the bipolar sensory neurones entering into contact with sense cells in Arthropods being real neurones.

[3]) PARSONS Introduction to the theory of perception. Cambridge psycho-logical library, 1927.

[4]) E. HOLMGREN. Zur Kenntniss des Hautnervensystems der Arthropoden. Anat. Anzeiger Bnd. 12, 1896, see also Bnd. 14, 1898.

Nusbaum [1]) and Schreiber) in the skin of crustacea (fig. 30) though confusion with connective cells makes such observations difficult.

Peripheral ganglia certainly occur in the *sympathetic system* of these animals, which has a similar structure as in vertebrates, consisting of *praeganglionic* and *postganglionic motor* neurones, while its sensory neurones run directly to the central system (Orlov) [2]).

The praeganglionic fibers arise partly in the tritocerebrum and para-oesophageal ganglia, partly in the posterior abdominal ganglion (Keim, Alexandrowicz) [3]). Postganglionic primitive ganglion cells are located on the viscera (cf. fig. 46).

Moreover, in the visceral plexus of Astacus, Alexandrowicz found bipolar sensory cells, sending one offshoot into the epithelium of the mucosa and their neurite into the muscles of the intestine, thus establishing a peripheral reflex arc (see also pag. 83).

The ventral cord of crustacea.

The relations in the *ventral cord* of crustaceans have been very carefully examined by Allen [4]), Bethe [5]), and Retzius [6]), who used the Golgi and methylene blue methods.

I shall merely give some notes concerning its principal constituents, starting with the *motor roots*, which generally arise from unipolar cells (fig. 31).

In some crustaceans, for instance Palaemon, but not in Astacus or Homarus, the neurite of these cells show the interesting feature

---

[1]) Nusbaum. Beiträge zur Kenntniss der Innervation des Gefäszsystems nebst einigen Bemerkungen über das subepidermale Nervengeflecht bei den Crustacëen. Biol. Centralbl., Bnd. 19, 1899. Nusbaum u. Schreiber. Beitrag zur Kenntnis der peripherischen Nervensystems bei den Crustacëen. Biolog. Centralblatt Bnd. 17, 1897.

[2]) Orlov. Das Magenganglion des Fluszkrebses. Ein Beitrag zur vergleichenden Anatomie des sympathischen Nervensystems. Jahrb. f. Morph. und mikr. Anat. Abt. 2 Bnd. 8, 1927.

[3]) Alexandrowicz Zur Kenntnis des sympathischen Nervensystems der Crustacëen. Jenaïsche Zeitschr. f. Naturw., Bnd. 45, 1909.

[4]) Allen. Studies on the nervous system of Crustacea. Quarterly Journ. of microsc. science. Vol. 36, 1894 and Vol. 39, 1897.

[5]) Bethe. Studien über das Zentrallnervensystem von Carcinus maenas. Arch. f. micr. Anat. Bnd. 44, 1895, see also Bnd. 50 and 51 ibidem, 1897 and 1898.

[6]) Retzius. Zur Kenntniss des Nervensystems der Crustacëen. Biologische Untersuch. N. F. Bnd. 1, 1890, see also ibidem Bnd. 7, 1895 and Bnd. 13, 1907.

in that some of them are surrounded by *myeline sheaths*. This also
may be regarded as a higher evolution, since we know that such
neurites have a much greater rapidity of conduction than have un-
myelinated nerve fibers (see page 14).

RETZIUS, to whom we owe this observation (l. c.), found these sheaths
to be divided into segments by annular constrictions resembling exactly the
rings of Ranvier in vertebrate myelinated nerves. Just as in vertebrates,
here also a nucleus appears in the midst of each segment, which therefore
seems to be provided with a lemnoblast sheath.

It may also be that the peripheral part of the nerve is a chain of cells,
in which conducting fibrillae are formed so that the lemnoblast is not an extra
cell surrounding the offshoot of a ganglion cell, but the very generator of the
neurofibrillae that are included in it. This "chain theory of nerve formation"
is strongly maintained by APATHY [1]) in his classic work on invertebrate neu-
rology and by HERINGA [2]) in vertebrates.

Nearly all motor fibers end directly in muscles, not in ganglia,
and run homolaterally. In Homarus, (fig. 31), ALLEN observed some
crossing rootfibers as well, while in the crab, BETHE found motor
root cells which send dendrites to the opposite side, subserving
crossed as well as homolateral reflexes.

Some cells have a dichotomizing neurite, the branches of which
run in different roots (fig. 31 left side), a condition similar to
that found in Annelids (cf. fig. 18). Other neurites originate in
the ganglion of one segment, then run longitudinally and emerge
through the root of another segment, as probably also occurs in
Annelids [3]). Next to these, and perhaps related to them, are root fibers
originating as collaterals of longitudinal tracts, so that several
segments may have collateral roots of one neurite. It is even said
that some of the *neurochords* in Arthropods give off collateral root
fibers (RETZIUS). Similar relationships were seen, though very
exceptionally, in Annelids (p. 34), and in young larvae of Amphibia
(HERRICK and COGHILL).

---

[1]) APATHY, Das leitende Element des Nervensystems. Mitteil a. d. Zool.
Station in Neapel. Bnd. 12, 1897.

[2]) HERINGA, The intraprotoplasmatic position of the neurofibrils in the
axon and in the endorgan. Proceed. Kon. Akad. v. Wetenschappen, Amster-
dam, Deel 25, 1917.

[3]) A similar course is observed in vertebrates by BERKELBACH with some
neurites of the XII nucleus which leave through the first cervical root.

The *sensory nerve roots* contain two sorts of fibers: neurites of neurosensory cells, and neurites of bipolar cells, whose dendrites either terminate freely in the skin or enter sense cells (p. 56). As in Annelids (fig. 18) most bipolar neurones of the sensory roots keep a peripheral position, but some sensory cells are located in the central nervous system.

The same is observed in Amphioxus (see p. 76), where some sensory root-cells lie inside the cord while others lie in the peripheral nerves.

The neurites of these cells end homolaterally, often dichotomizing into an ascending and descending branch and passing through several ganglia (fig. 31, S R F).

Probably some sensory root fibers decussate or send collaterals on the other side.

It should be emphasized that, as in most invertebrates, the ventral cord roots generally contain sensory as well as motor fibers.

Though it is customary to speak of anterior and posterior roots in crustacea, these roots may 'by no means' be compared to the vertebrate ventral and dorsal roots. They are better called oral and caudal roots. Each segment usually has two roots which do not leave the ganglia underneath each other, but in front of each other.

The anterior (oral) root generally goes to the body wall, the posterior (caudal) one to the extremities, but generally both contain sensory as well as motor fibers.

Pure motor and sensory roots occur in protracheata and in insects, and here the dorsal root is usually motor and the ventral root sensory, just the reverse of what is observed in vertebrates.

The *secondary neurones* are very numerous in crustacea. Most of them are unipolar cells, as is usually the case in higher invertebrates, their cells lying at the periphery of the neuropilema. There are ascending, intra ganglionic and descending secondary neurones.

Some of the *ascending neurones* are very long, for instance, those connecting the abdominal ganglia with the brain ganglia. Intraganglionic neurones are second type cells (similar to fig. 25 *b*.).

Among the *descending neurones* we may distinguish short ones, connecting only a few segments, and long ones running the length of the cord and sometimes giving collaterals to the ganglia which they pass.
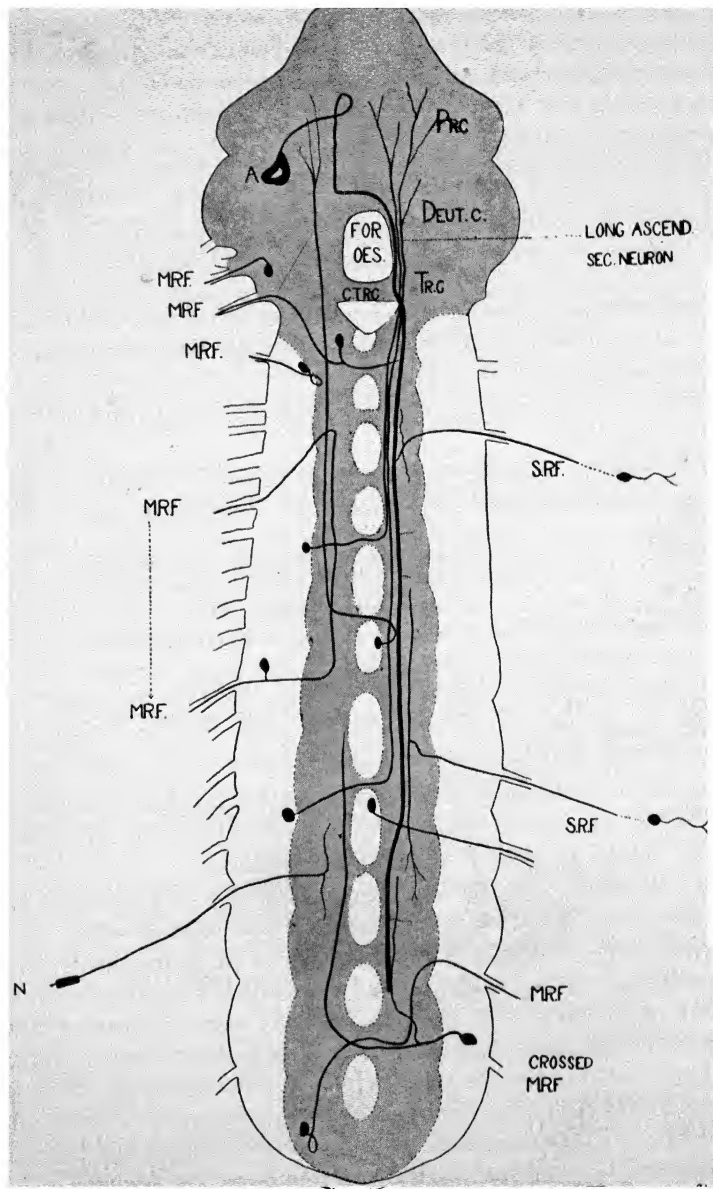
Fig. 31. Brain ganglion and ventral cord in a larva of Homarus after ALLEN (modified). PRC = protocerebrum. DEUT. C. = deuterocerebrum. TR. C. = tritocerebrum. FOR. OES = foramen oesophageale. C. TR. C. = Commissure of the tritocerebrum. M.R.F. = motor root fibers. S.R F. = sensory root fibers (bipolar neurones). A. = Neurochord cell. N = Neurosensory cell. Central sensory root cells are not drawn.

The first sort of connection has the character of a chain reflex path, as occurs in worms, where a contraction in one segment is gradually followed by contractions of the following segments. Among the long descending neurones real *neurochords* occur, originating in the brain (A, fig. 31) and terminating, after decussation, far caudally. According to RETZIUS, they may even leave the ventral cord at its caudal end, and enter the muscles of the tail. This has, however, not been confirmed.

The ventral cord of insects.

The *ventral cord of insects* resembles, in its principle features, that of the higher crustacea. For the latest literature on this subject I refer to the papers of HILTON [1]), and ZAWARZIN [2]) (for the protrachreate Peripatus see FEDOROW [3]).

Some differences, however, should be mentioned. So real neurochords have not been observed in insects, as far as I know, though long descending tracts, arising in the cerebrum, are found running through the whole ventral cord. Of greater importance is *the differentiation into motor and sensory roots in protracheata and in insects.* In the suboesophageal ganglion the motor root cells lie ventrally, the dorsal cells being secondary neurones subserving motor correlations (KENYON [4]). But in the thoracic and abdominal ganglia the *dorsal* cells and roots are *motor*, while the *ventral* roots are all *sensory* (FAIVRE, BINET, ZAWARZIN and FEDOROW), *the reverse of what is found in the spinal cord of vertebrates.*

As, however, the ventral side of the cord in invertebrates is nearest to the skin, as the dorsal side is in vertebrates, this reversed condition is easily explained by the neurobiotactic influence of the skin.

---

[1]) HILTON. Afferent and efferent pathways in an abdominal segment of an insect. Journ. of comp. Neurol. Vol. 36. 1924.

[2]) ZAWARZIN. Zur Morphologie der Nervenzentren. Das Bauchmark der Insecten. Beitrag zur vergleichenden Histologie. Zeitschr. f. wiss. Zoologie Bnd. 122, 1924.

[3]) FEDOROW. Zur Anatomie des Nervensystems von Peripatus, Zool. Jahrb. Abt. f. Anat. und Ontogenie, Bnd. 48, 1926.

[4]) KENYON. The brain of the bee. Journ. of Comp. Neurology, Vol. 6, 1896.

The brain ganglion.

The cerebrum of *insects* (fig. 33) is constructed on the same plan as that of the crustacea, but differs from the latter by the *constant* possession of *corpora pedunculata* or *globuli* (mushroom-bodies), which do not occur in all crustacea, though HAUSTRÖM [1]) showed their presence in some malacostracs (Calocaris, fig. 32).

BETHE thought that such globuli occur also in Carcinus maenas, but HOLMGREN [2]) and others proved that there is no reason to believe so, since it appears from BETHE's own researches that the centres which he took for mushroom bodies receive the first antennal or olfactory nerve and lie in the deuterocerebrum, while the corpora pedunculata always belong to the protocerebrum.

The *corpora pedunculata*, or *globuli*, in insects as well as in Calocaris consist of a cap of cells, underneath which there is a dense neuropilema. Their development varies, but they are generally very large in insects with highly correlated functions.

In wasps they attain a very large size in the socially living forms. Among bees they are most highly developed in the workers, as is also the case in ants, where, according to HANSTRÖM [3]), they constitute 42% of the volume of the brain (in other insects only 1,2—10%).

On the other hand, in humble-bees and wasps, they are largest in the queen, which according to PLATE, may be connected with the fact that in the spring the queen does all the work for the foundation of new colonies. Apparently the corpora pedunculata have to do with highly correlated functions. This has also been shown experi-

---

[1]) HANSTRÖM. The olfactory centres in Crustaceans; Journ. of Comp. Neurology, Vol. 38, 1925.

[2]) N. HOLMGREN. Zur vergleichenden Anatomie des Gehirns von Crustaceen. Kongl. Svenska Vetenskaps Akademiens handl. Bnd. 56, 1916.

[3]) In Decapods it varies from 10—30 %, in Arachnoids from 10—50 % but in Limulus it even amounts to 80 %. In these calculations also the central body is included; c.f. HANSTRÖM: Untersuchungen über die relative Grösse der Gehirnzentren verschiedener Arthropoden etc.; Jahrb. f. Morph. und mikr. Anat. Bnd. 7, 1926 and *the same:* Das Nervensystem und die Sinnesorgane von Limulus polyphemus; Kungl. Fysiografiska Sällskapetts Handlingar, N. F. Bnd. 37 N°. 5, 1926.
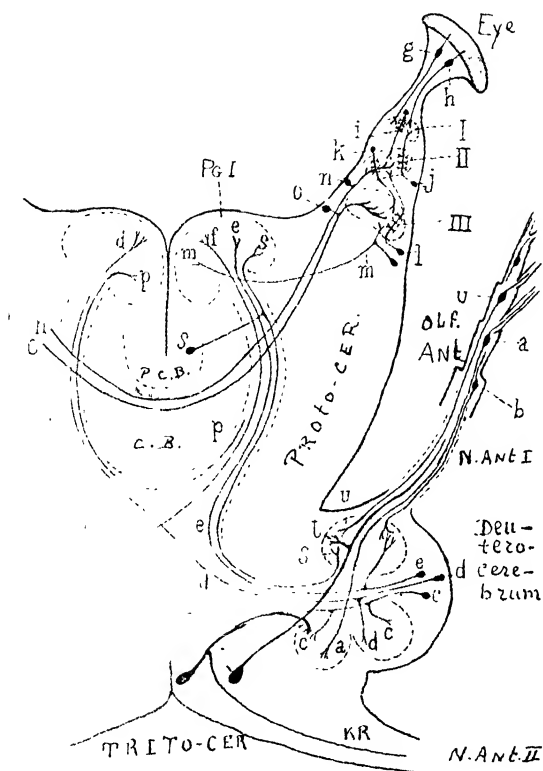
Fig. 32. Brain ganglion of a crustacean (Calocaris) after Hanström, Journ. of Comp. Neur. Vol. 38, 1925. — The eye stalk of the protocerebrum contains three optic synapses or medullae (I, II, III); g and h = visual neurosensory cells ending in the first medulla; i, j, k and l intercalating neurones of the medullae; m connects the third medulla with the mesial mushroom body or corpus pedunculatum (P. G. I; also lateral mushroom bodies — c. f. fig. 33 — occur here, but are not drawn). n. o. = optic commissure; p = commissural fiber of the mushroom bodies running in their peduncles (p), which also contain crossed (f, d) and uncrossed (e, s) connections with the glomeruli olfactorii (u in the deuterocerebrum). Olfactory cells (u, a, b) of the first antenna send their neurites in these glomeruli. c = olfactory commissure. Motor neurones of the tritocerebrum (t and kr in the tritocerebrum) transmit homolateral impulses (t) to the muscles of the first (olfactory) antenna and crossed impulses to the muscles of the 2d (non olfactory) antenna (N. ant. II). P. C. B. = protocerebral bridge; C. B. = central body.

mentally. After their removal some instincts are disturbed, as the
courting instinct and the proper care of eggs.

Insects generally have two pairs, arachnoïds one pair of mushroom bodies [1]).
Only the Phalangides have three pairs.

The protocerebrum, in which the corpora pedunculata lie, is
entirely optic and associative in character. The deutero- and trito-
cerebrum are sensory and motor, the deuterocerebrum receiving
olfactory impulses and sending motor roots to the antennae, while
the tritocerebrum receives ordinary sensory fibers and sends motor
roots to the labrum and into the sympathetic system.

From the deuterocerebrum or olfactory antennal ganglion (see fig. 33),
arises the nerv. antennarius sensibilis, (n. ant. s.) or n. olfactorius together
with the n. antennarius motorius externus (n. ant. m. o.).

Behind this the n. antennarius motorius internus leaves the deutero-
cerebrum, though its root-cells lie partly in the tritocerebrum, where the
mixed nerv. labralis also originates and ends.

This part of the cerebrum is connected, by the perioesophageal ring,
(very short in bees) with the infra-oesophageal ganglia, which give origin to
a large number of nerves, the mixed mandibular, maxillar and labial nerves,
behind which the n. n. posteriores originate. The infra-oesophageal ganglion
finally continues in the ventral cord.

The protocerebrum of insects is connected with two *optic systems*,
the *ocelli*, and the compound *facet eyes*. Of the three ocelli (oc.),
the middle one is connected with the *pons* and *central corpuscle*,
where it acquires relations with optic impressions from the com-
pound eyes, and also with impulses from the deuterocerebrum
(in which in the olfactory antenna ends). The lateral ocelli,
according to KENYON, send their neurites, partly directly, into the
oesophageal ganglion and ventral cord. Around and above the
neuropilema of the pons and the central body are central motor
cells which, at least in Periplaneta, according to BRETSCHNEIDER [2]),
act, probably indirectly (though the connection is drawn as a direct
one in figure 33), on the nuclei of the motor antennal nerves and,
further down on motor nuclei of the oesophageal ganglion and
ventral cord.

---

[1]) GOTTLIEB. Ueber das Gehirn des Skorpions. Zeitschr. f. Wiss. Zool.,
Bnd. 127, 1926.

[2]) BRETSCHNEIDER. Ueber die Gehirne der Küchenschabe und des Mehl-
käfers. Jenaische Zeitschrift für Naturwissensch., Bnd. 52, 1914.

PLATE III
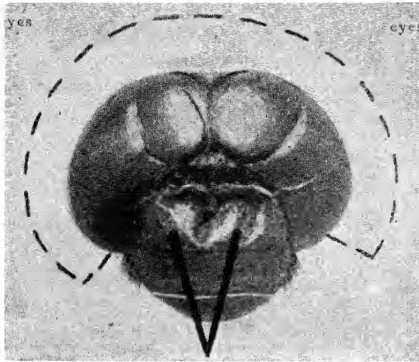
Head.
Head and facet eyes of Aeschna grandis.
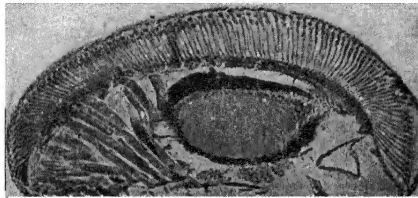
Facet eye of Musca.
(PEETERS).
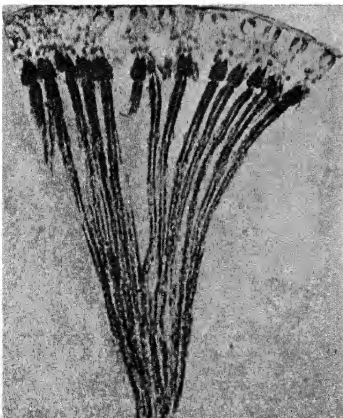
Longitudinal section.
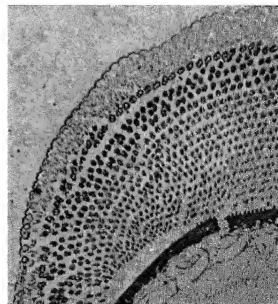
Transverse section.

RHABDOMS OF AESCHNA.
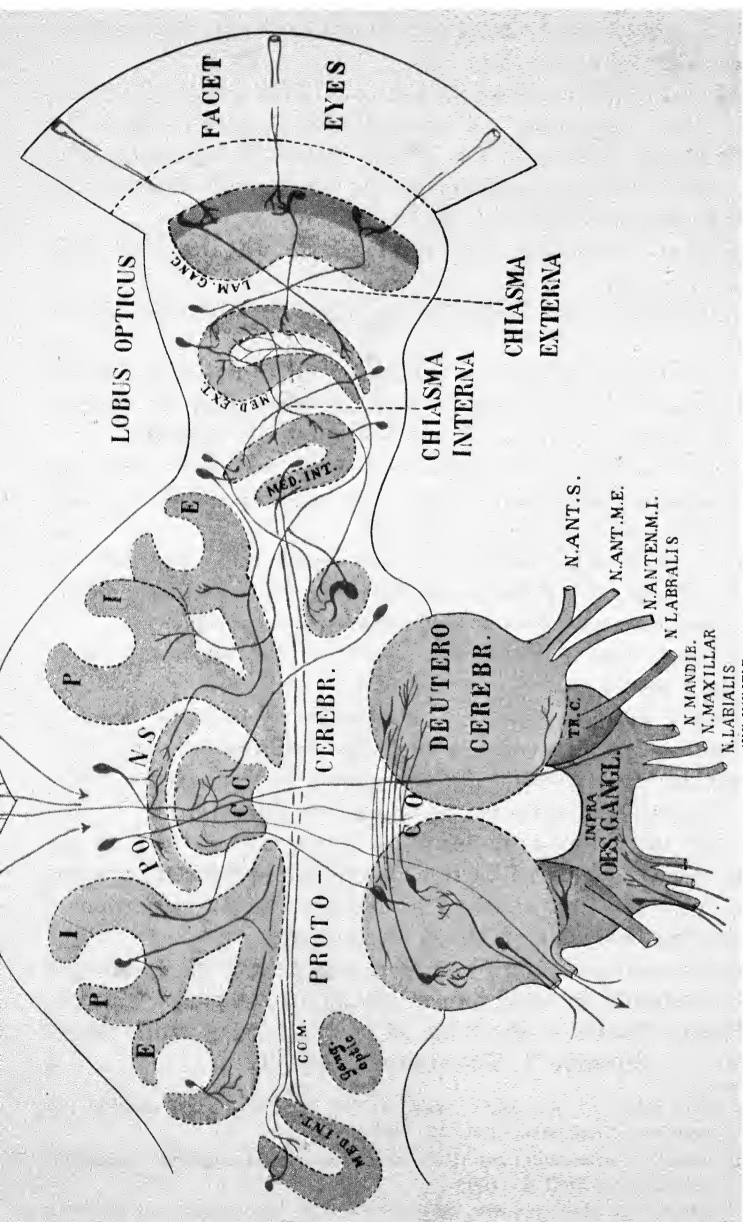
Fig. 33. Connections of the oesophageal ganglia, brain and optic lobe of the bee, chiefly after KENYON. The contours of the brain ganglia are drawn after JONESCU's waxreconstructions. Use has been made of FORTUYN's survey. Of the commissures the olfactory commissure (co.) between the deuterocerebra and the commissural connections between the left and right medullae internae (med. int.) of the optic lobe (com.) are drawn, the commissure between the corpora pedunculata is partly indicated on the left side. The pons (po....ns) and central corpuscle (C.C.) are drawn too large.

It thus appears that the pons and central corpuscle are *correlation centers* for the ocelli and facet eyes.

For the arrangement of the optic neurones of the compound or facet eyes and their "medullae" (= neuropilemae) I refer to figure 33.

An interesting feature is the double chiasm in the optic lobe, one between the lamina ganglionaris and the medulla externa, and the other between the latter and the medulla interna.

The *corpora pedunculata* also receive optic impulses, but from the facet eyes only.

This connection is established in two ways (see the right side of figure 33).

One connection is formed by cells lying on the medulla interna and branching in its neuropilema, and the other with the medulla externa by means of cells in or near the ganglion opticum.

Besides the corpora pedunculata receive olfactory fibers from the antennal ganglia (deuterocerebrum), and are connected by commissural fibres, as in Calocaris (fig. 32).

KENYON could trace neurites of the mushroom cells into the peduncles, giving off collaterals on their way. But the final destination of these efferent fibers is not sufficiently studied.

Perhaps they run to the motor centers of the antennae and to ventral cord nuclei.

In addition to connections with the corpora pedunculata, commissural fibers occur between the medullae internae of both sides. They are generally divided into two parts: the *commissura optica superior* and *inferior* (indicated as one in my figure).

That the deuterocerebrum also has a commissure (two in the bee) was mentioned in the general description of the head ganglia. We may consider this olfactory commissure as an indication of the segmented character of the deuterocerebrum.

The commissure of the tritocerebrum runs behind the oesophagus in most crustacea, in some insects and in all arachnoids (fig. 29).

For further details on the brain of insects I refer to the papers of KENYON [1]), JONESCU [2]), THOMPSON [3]) and others.

[1]) The optic lobes of the bee's brain in the light of recent neurological methods. American Naturalist, Vol. 31, 1897.

[2]) Vergleichende Untersuchungen über das Gehirn der Honigbiene. Jenaische Zeitschr. f. Naturwiss. Bnd 45 1909.

[3]) The mushroom bodies of ants. Journ. of Comp. Neurologie vol 23, 1913.

PROCHORDATA.

Hitherto, I have dealt with invertebrates, in which the larger part of the central nervous system, the cord, lies at the ventral side of the body under the intestinal tract. We have seen though, that this condition is not the most primitive one. In flatworms (see p. 26), a part of this system arises from the dorsal side of the body, forming dorsal strings, and another part from the lateral and ventral sides, forming lateral and ventral strings.

From this it is evident that all parts of the ectoderm are able to produce not only epithelial and subepithelial nerve cells, but also central connectives.

Whereas, however, the dorsal and the lateral connectives gradually become of minor importance, the ventral ones (perhaps because of the crawling life of lower invertebrates) prevail to a greater and greater degree, finally joining and so forming the impair *ventral cord*, characteristic of most higher invertebrates.

Only the head ganglia always arise from the dorsal ectoderm (see fig. 16) and its connection with the ventral cord is established by the oesophageal ring or cerebro-pedal peduncle, as it is called in molluscs.

There are, however, two groups of invertebrates, the Enteropneusts and the Tunicates, in which the larger part or the whole of the central nervous system arises dorsally, and retains a position dorsal to the intestinal tract, thus introducing the condition found in vertebrates.

These two groups, moreover, have a primitive chorda dorsalis. and therefore are called *prochordata* [1]).

Enteropneusts.

The simplest form of *prochordata* are the Enteropneusts, also called, with BATESON [2]) and HARMER [3]), *hemichordata*, because of

[1]) DELAGE and HÉROUARD. Les Procordés. Traité de Zoologie concrète.

[2]) W. BATESON. On the morphology of the Enteropneusta. Quarterly Journal of microsc. Science. Vol. 25, 1885.

[3]) HARMER. The Pterobranchica of the Siboga expedition. Uitkomsten der Siboga expeditie etc. Deel XXVI*bis*, 1905.

the fact that their chorda is very primitive, and is represented chiefly by a fronto-dorsal diverticulum of the intestinum in the glans

frontal (glans or prostomium)

caudal (branchial region)

mouth
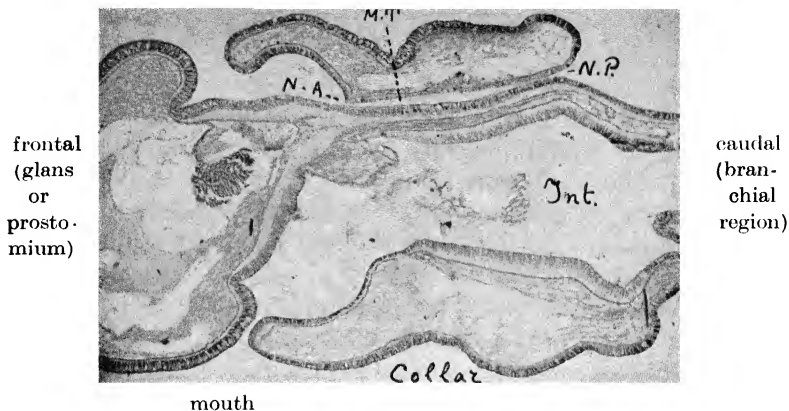
Fig. 34. Sagittal section through the collar region of Ptychodera bahamensis. M.T. = medullary tube; N.A. = neuroporus anterior; N.P. = neuroporus posterior. Photo by VAN DER HORST.

or prostomium. This continues in a ridge of cells (not visible in my sections) connected with the dorsal wall of the intestinum in the collar region and branchial region.

Their nervous system, carefully studied by KOWALEWSKY [1]), SPENGEL [2]), BATESON (l. c.) J. P. HILL [3]), and VAN DER HORST (l. c.), is very remarkable, since it represents a combination of vertebrate and invertebrate characteristics. The structural plan of the vertebrates is found in the collar region, immediately behind the glans (see fig. 34 and 35), the invertebrate type in the branchial and body region.

In the collar region a paired ectodermal fold arises, which, similarly as the neural fold of vertebrate embryos, later closes and thus forms a tube. This *medullary tube* separates from the dorsal ectoderm,

[1]) KOWALOWSKY, Anatomie von Balanoglossus. Mémoire de l'Académie de St. Petersbourg, 1866.

[2]) SPENGEL. Ueber den Bau und die Entwicklung der Balansglossus. Berichte der 50ten Versamml. der Deutschen Naturf. und Aerzte. München 1877.

[3]) J. P. HILL. A new species of Enteropneusts, Ptychodera austral. Linnean Soc. of New S. Wales. Vol. X, 1894.

leaving (Ptychodera, fig. 35, 36) a small connecting bridge, which, as a consequence of insufficient closure is sometimes hollow.

The frontal opening of this tube, in Ptychodera [1]), is called *neuroporus anterior*, and the caudal opening (behind the collar, fig. 36, left) *neuroporus posterior*, (SPENGEL [2]), WILLEY [3]).

The epithelium of the tube contains *neurosensory cells* and *supporting cells*. Under it SPENGEL and VAN DER HORST [4]) saw giant ganglion cells.

Also glandular cells have been found in it. This does not, however, interfere with the current interpretation of this tube, since glandular cells are also observed in the medullary tube of Petromyzon, sharks (SPEIDELL) and Teleosts (FAVARO). Cf. p. 105 and 121.
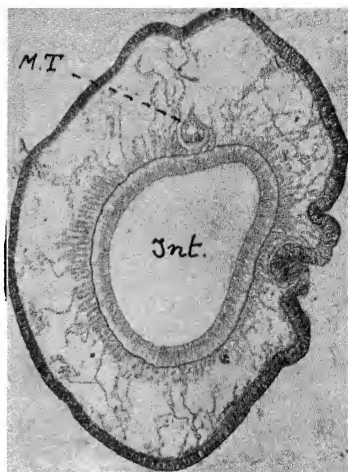
Fig. 35. Section through the collar region of Ptychodera bahamensis. M.T. medullary tube (its connecting bridge with the dorsal epithelium is broken). Int. = intestinum.
Photo by VAN DER HORST.

This cellular layer is surrounded by a distinct neuropilema reminding one of the *fiber mantle* in the spinal cord of vertebrate embryo's.

From these facts it appears that the arrangement in the collar region resembles the first closure of the medullary tube in young vertebrate embryos (comp. fig. 43).

----

[1]) The tube is not continuous in all enteropneusts. It is sometimes represented by separated small sacks.

[2]) In Balanoglossus apertas the neuropori are closed. (SPENGEL, 1893). See also Neue Beiträge zur Kenntnisz der Enteropneusten I Ptychodera flava Eschsch. von Laysan. Zool. Jahrbücher, Anal. Bnd. 18. Heft 2, 1903 and Studien über die Enteropneusten der Siboga Expedition. Monographie XXVI of the Siboga expedition. Brill, Leiden, 1907.

[3]) WILLEY. Enteropneusta in Willey's Zoological Results, Part III, 1899, Cambridge. See also his Remarks on some recent work on the protochordata. in the Journ. of micr. Science. Vol. 42, 1899. —

[4]) VAN DER HORST. Het zenuwstelsel der Hemichordaten. Psych. en Neurol. Bladen, Amsterdam, 1927.

The neurogenetic epithelium of the collar extends beyond the collar, frontally on the glans and caudally on the body, in the *dorsal midline* as an unclosed strand of cells, accompanied by a dense layer
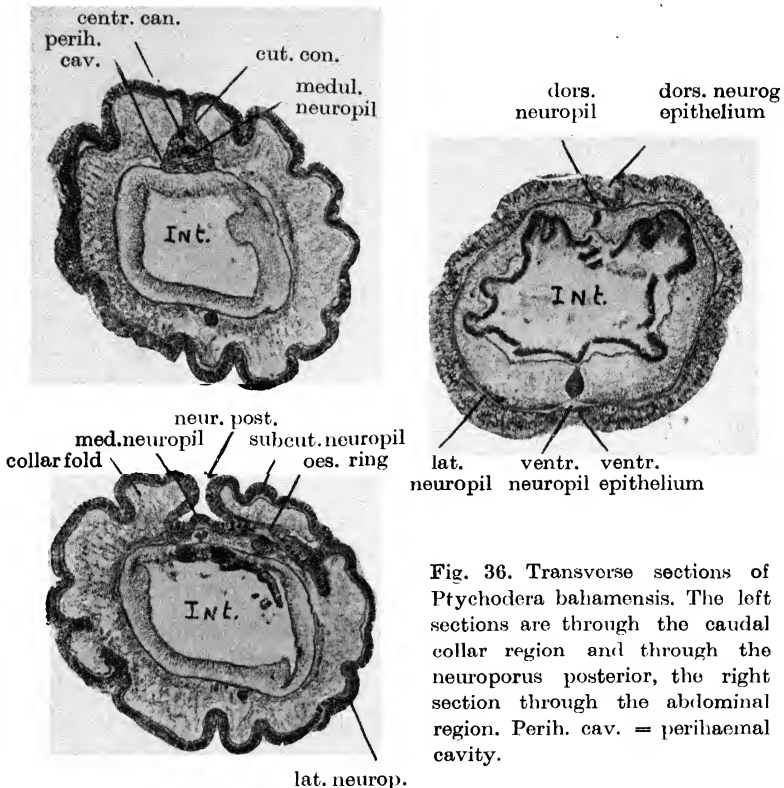
Fig. 36. Transverse sections of Ptychodera bahamensis. The left sections are through the caudal collar region and through the neuroporus posterior, the right section through the abdominal region. Perih. cav. = perihaemal cavity.

of neuropilema which continues in the basicpithelial fiber plexus [1] of the sidewalls.

The dorso median neurogenetic epithelium in front and behind the neuropori reminds us of the anterior and posterior unclosed parts of the medullary primordium in a 7—8 somite vertebrate embryo (fig. 43), the more so as it lies a little deeper than the adjoining ectoderm (see fig. 36, at the right).

Another column of neurogenetic ectoderm is found, however, on the *ventral midline* of the body, resembling in all points the dorsal

---

[1] Such a basiepithelial plexus also occurs under the ectoderm of the collar.

neurogenetic line. It is, likewise, accompanied by a neuropilema, which again extends in the basi-epithelial plexus of the side walls, meeting the lateral extension of the dorsal pilema.

This neurogenetic epithelium contains also neurosensory cells and ganglion cells (Köhler, Schneider, and Spengel). In addition supporting cells occur in it.

Connections of its neuropilema with the underlying muscle layer were observed by Bateson.

Finally the dorsal neurogenetic epithelium behind the collar is connected with the ventral one by a dense ring of neurogenetic epithelium and neuropilema, surrounding the pharynx (fig. 36, left), establishing a primitive homologue of the *oesophageal ring* (Spengel).

We consequently find in the Enteropneusts both types of the nervous system, the invertebrate and vertebrate type, the former being repre-sented by the oesophageal ring and ventro-median neuroepithelium, the latter by the medullary tube in the collar and by the frontal and caudal dorso-medial neuroepithelium.
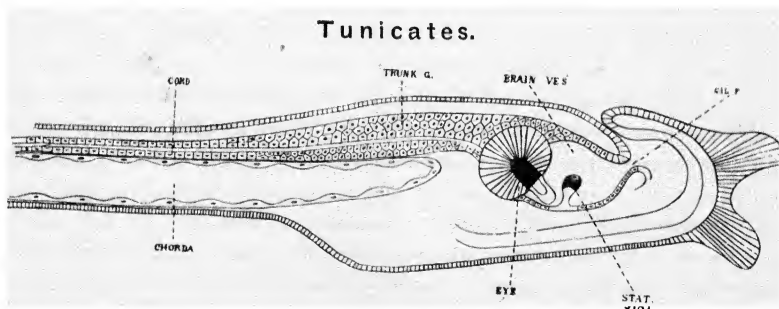
Fig. 37. Sagittal section of the larva of Phallusia mammillata, after Kowalesky.

In Tunicates the ventral primordium of the nervous system dis-appears and the dorsal medullary plate closes over the whole length of the body, except at the frontal end.

The central nervous system of the *ascidian larva* may be divided into three parts, a thin caudal part or *cord*, a broader middle part or *trunk*, and a frontal part or *sense vesicle*. Of these the cord and the larger part of the trunk lie upon the chorda (fig. 37).

The vesicle is entirely praechordal and opens into the pharynx by a ciliated furrow (fig. 37, cil. f.), a sense organ (Hunter), probably the homologue of the infundibular organ of Amphioxus (Dammer-

MAN [1])). Dorsally to it lies the neuroporus anterior [2]) that secondarily connects with the pharynx (see fig. 37).

Behind the ciliated groove lies an endocrine gland, also developed from the neural tube and generally compared to the pars infundibularis hypophyseos [3]).

In the vesicle two sense organs occur; an asymmetric *eye* (at the right) and a *statocyst* (at the bottom), the connections of whose neurites, however, are unknown.

Also concerning the connections of the other parts of the nervous system in these larvae no data are available.

Only in *Appendicularia*, where this form is retained in the adult, fibers connecting the cord with the adjacent musculature have been observed, and it is said that they have a metameric arrangement.

In the adult sessile Ascidia the nervous system is much reduced.

CHORDATA [4]).

Amphioxus.

The central nervous system of Amphioxus, which has a well developed chorda but no vertebrae, resembles that in vertebrates.

There is, however, a simplicity of structure here, by which it remains far below the differentiation even in the lowest fishes.

The whole central nervous system arises ontogenetically from an infolding of the dorsal ectoderm, and frontally remains in open contact with it at the olfactory pit, which is a direct continuation of the ectoderm in the anterior neuroporus (see fig. 39).

The chorda in Amphioxus also extends underneath and even beyond the brain vesicle, contrary to the condition found in Tunicates and Vertebrates.

---

[1]) DAMMERMAN. Der Saccus vasculosus der Fische ein Tieforgan. Zeitschr. f. wiss. Zoologie Bnd. 96, 1910, p. 689.

[2]) In comparison to the Enteropneusts the neuroporus anterior is shifted frontally in Tunicates as it also does in embryos of vertebrates.

The praechordal position of this vesicle and the epichordal position of the collar tube of Enteropneusts seem to confirm this supposition.

[3]) METCALF. Note on the morphology of the Tunicata. Zool. Jahrb. Abt. f. Ontog. und Anat. Bnd XIII, 1900. Cf. also FRANZ, Morphologie der Akranier. Ergebn. der Anatomie und Entwickl. Bnd. 27, 1927 (p. 660).

[4]) For the literature on the nervous system of Amphioxus and Vertebrates I refer to my book "Die vergleichende Anatomie des Nervensystems der Wirbeltiere und des Menschen", Bohn, Haarlem, 1920 and 1921.

Some authors consider the subcerebral part of the chorda as the homologue of the frontal chorda of Enteropneusts. I am inclined to consider it an elongation proper to this animal and due to the support needed by the head region, when the animal pierces the sand with its head.

In the adult the spinal cord retains the form of a tube, but its lumen acquires the shape of a vertical split.
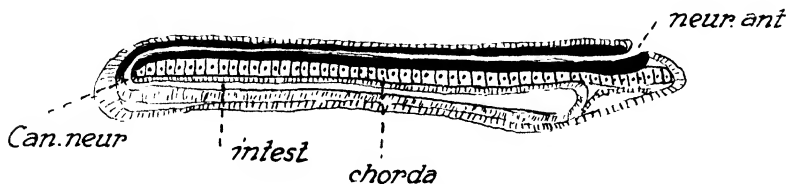
Fig. 38. Larva of Amphioxus after HATSCHEK (medullary tube black).

The dorsal or *roof plate* of this canal, well developed in the spinal region, becomes thinner in a frontal area (about the level of the second dorsal nerve) and extends as a single cell layer to the forebrain vesicle, thus reminding one of a small *choroid roof*. On top of this choroid lies a group of large cells (cells of JOSEPH, Fig. 39).

Then the ventricle widens, forming the *brainvesicle*, in the caudal part of which, at the bottom, the *infundibular sense organ* is seen (fig. 39). Since we know (BOEKE) that this organ corresponds to the sense organ in the saccus vasculosus [1]) of fishes, we may conclude that the level of its position corresponds with the hindborder of the tweenbrain in fishes.

This and all that lies in front of it is the primitive forebrain, or *prosencephalon* [2]) (forebrain + tweenbrain), and the region behind it (covered by the cells of Joseph) is the *deuterencephalon* [2]) (midbrain + oblongata in fishes). The latter continues into the spinal cord.

The Prosencephalon.

The brain vesicle is chiefly a sense vesicle, though not of static and optic impulses as in Tunicates. Frontally, it is connected with a ciliated groove which by most authors is considered as an *impair olfactory organ*. (FRANZ, l.c. supra, is opposed to this view).

Underneath the entrance of the impair olfactory nerve, *pigment*

---

[1]) As the neurosensory hairs extend in the ventricle, this organ probably has to do with the perception of intracerebral pressure.

[2]) It is evident that this expression does not involve a homology with the protocerebrum and deuterocerebrum of Arthropods.

cells occur, which, perhaps, may be the reminiscence of an eye, but which are not sensitive to light, not being accompanied by light percipient neurosensory cells. Again underneath them, in the ventrofrontal wall of the vesicle, the paired sensory *N. terminalis* enters the basis of the prosencephalon (VAN WIJHE).
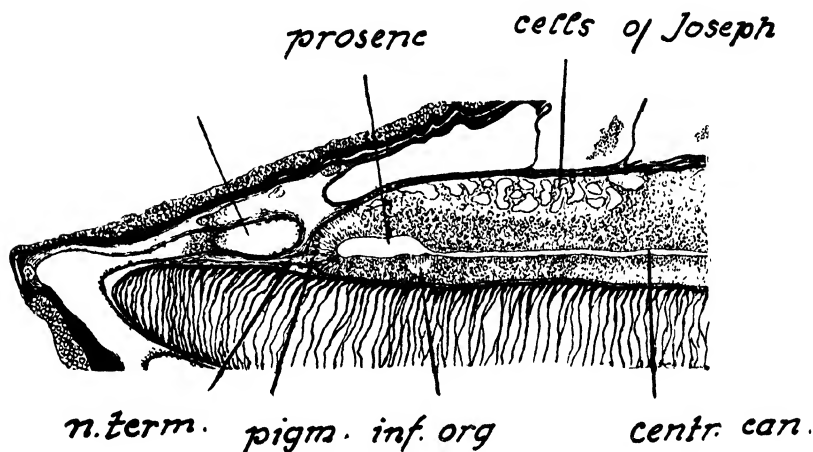
Fig. 39. Paramedian sagittal section of the frontal region of Amphioxus. The membranous roof underneath the cells of Joseph is not seen, the section not being made in the median line.

An infundibular hypophyseal sac does not occur, but the mouth part of the *hypophysis* may be represented by the *preoral groove*, which has the same relations to the praemandibular somites as the *pars tuberalis hypophyseos* of TILNEY (DE BEER [1]).

Deuterencephalon.

The region immediately behind the prosencephalon, representing the midbrain and oblongata of fishes is very simple, being characterized only by the cells of Joseph, which probably are neurosensory cells, their peripheral protoplasm having a striped (palissaded) character (BOEKE), as is sometimes observed in the light percipient cells of invertebrates. Their function, however, is unknown. As they are not sensitive to light, they may represent a static sense organ but this is a mere supposition.

[1]) DE BEER. Die Geschichte der Pars tuberalis der Pituitardrüse. Anat. Anzeiger, Bnd. 60, 1925.

In the deuterencephalon enter two dorsal nerves, which probably represent the primitive homologues of the two nerves from which the trigeminus arises [1]) in vertebrates, with this difference though, that they are purely sensory, containing both skin, and, the second nerve, also viscero-sensory fibers. They do not contain motor fibers as does the trigeminus of vertebrates (cf. p. 106).

There are no ventral roots in this region [2]).

Behind the second dorsal root the central canal narrows, and thus a sort of *calamus scriptorius* occurs. About the half of the medulla, behind the second dorsal root is more or less homologous to the facial, glossopharyngeal and vagus region of fishes, but its nerves do not show much difference from the more caudal nerves.

In the whole medulla, the dorsal roots alternate with the motor roots.

This alternation [3]) is to be explained by the fact that the sensory roots run through the intermuscular septa, the ventral roots ending in the myotomes.

The *dorsal roots* in the spinal cord contain

Fig. 40. Spinal cord of Amphioxus with sensory root (R.post.) and giant ganglion cell (G.c.).

somato- and viscero-sensory and viscero-motor fibers.

The sensory fibers arise partly from bipolar ganglion cells in the cord, and partly from cells that lie peripherally in the nerves, as also occurs in invertebrates (cf. p. 34 and 59).

In still another respect some of these roots resemble those of inverte-

---

[1]) The trigeminus ontogenetically corresponds with two neuromeres, the N. ophthalmicus being originally connected with the second midbrain neuromere and the N. maxillo-mandibularis with the second rhombomere.

[2]) In fishes, in this region the oculomotor nerve arises ventrally, but as there are no frontal eyes in Amphioxus, this root is lacking.

[3]) Another alternation takes place between the roots of the left and right side. This is due to a shifting of the left side of the body. the left first gill-pouch having become a mouth. (VAN WIJHE). —

brates, as they contain also (FORTUYN) neurites of neurosensory cells.

Centrally, the *cutaneous* and *proprioceptive* (musculo-sensory) *fibers* dichotomize into ascending and descending branches. Most of them remain on the same side, but crossing sensory rootfibers are observed.
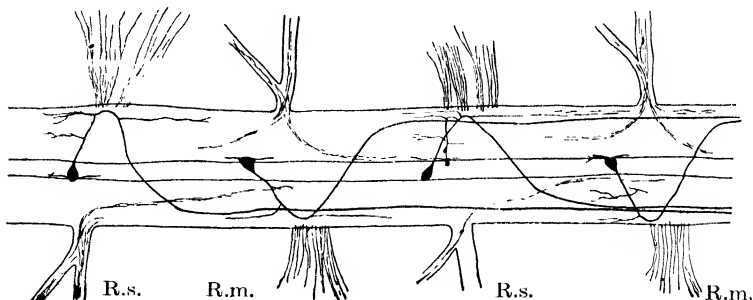
Fig. 41.‾ Schematic representation of the position of the giant cells in Amphioxus, and the course of their fibres (RETZIUS). R.s. = Radices sensibiles; R.m. = radices motoriae.

The *viscero-sensory fibers* have only descending branches (JOHNSTON). The *visceromotor fibers* of the dorsal roots innervate the perivisceral musculature of the intestinum. They may perhaps be compared to vagus fibers, the more so as they are lacking in the caudal roots.

The *ventral roots* contain motor fibers for *three* adjacent myotomes [1]), but most of the fibers enter the middle myotome. They further contain sympathetic fibers for the vascular system [2]) (AYERS).

The somatomotor fibers may arise from cells lying near the central canal, at some distance from the roots, but the possibility is not excluded that they arise, partly at least, as collaterals of longitudinal fibers, as sometimes occurs in the invertebrates (p. 34 and 58), and as is observed in larvae of Amphibia by HERRICK and COGHILL.

Of the *secondary neurones*, the smaller cells are arranged around the central canal. Their neurites descend as well as ascend. Very large secondary neurones are the *giant cells* (fig. 40 and 41), lying in the dorsal midline, their cell bodies extending on to both sides of the midline. They form a frontal and a caudal group.

The frontal group lies between the levels of the sixth and ninth nerves, one cell corresponding with each sensory root.

---

[1]) In Petromyzon JOHNSTON also observed roots innervating more than one myotome.

[2]) The presence of postganglionic autonomic cells is doubted by VAN WIJHE.

In the tenth to fourtieth segments no giant cells occur, but between the fourtieth and sixtieth root each segment again contains one giant cell.

This pattern of localization of the giant cells reminds us of the situation in Annelids, as described by ASHWORTH (vide p. 36).

That no cells of this character develop in the middle segments (as is also the case in Annelids) is due to the fact that the middle part of the body is the least sensitive. Accordingly most reflexes originate from the frontal and caudal ends (PARKER).

The frontal cells send their neurites backward, the caudal cells frontally, always alternatingly on the left and right sides of the cord, and crossing underneath the central canal. The striking fact that the localization of these cells always corresponds to a sensory root shows the influence of these roots on their develop-

Fig. 42. Showing the dorsally looking "eyes" (A) on the left, and the ventrally looking "eyes" (B) on the right side, and underneath the central canal (c.c.).

ment, which is also proved by their prevailing occurrence in the (most sensitive) frontal and caudal regions. This is, again, an example of the fact that the topography of cells is determined by the impulses that act on them (neurobiotaxis).

A striking feature of Amphioxus is the occurrence of numerous *light percipient* cells in the ventral part of the cord, underneath the central canal. Those on the right side of the canal "look"

ventrally: those on the left dorsally. As, however, the animal
usually lies on its side, it perceives the light of a horizontal plane.

These eyes, reminding us of the solitary eyes in Haemopis (Plate I),
consist of one (or two) cap-like pigment cells, and one light percipient
cell (fig. 42), provided with neurofibrillae (BOEKE). The further course
and ending of their neurite is however as yet unknown.

Other *neurosensory cells* lie in the ependyma of the central canal
(EDINGER, STENDELL). Their neurites join and proceed into the
cord. This occurrence of neurosensory cells in the ependymal epithe-
lium of the central canal is not strange, when we consider the fact
that the medullary tube arises from the neurogenetic ectoderm,
which, in all invertebrates (especially in Enteropneusts) is richly
provided with neurosensory cells.

Reviewing the structure of the nervous system of Amphioxus we find
that, though much more highly developed than that of Enteropneusts
and Tunicates, in many respects it is still very primitive. The brain
vesicle is unpaired. A secondary forebrain and a 'tweenbrain are not
differentiated, both being included in the primitive prosencephalon
or archencephalon. In the deuterencephalon no midbrain and
oblongata are differentiated. It is characterized by the cells of Joseph,
not occurring in fishes. The primitive choroid roof underneath
these cells probably represents in a primitive way the choroid of
both the midbrain and oblongata of Petromyzon.

The optic and eye muscle nerves are failing. Of the dorsal nerves
in this region the first probably represents the mesencephalic (opthal-
mic) trigeminus root[1], the second its rhombomeric root. The following
dorsal nerves may represent the facial, glossopharyngeal and vagus
nerves of vertebrates, but do not differ from the spinal dorsal
nerves, containing, in addition to viscero-sensory and viscero-motor
fibers, a great many cutaneous fibers.

In the *spinal cord*, the neurosensory ependymal cells, simple eye-
cells and giant neurones remind us of primitive conditions. as does
also the fact that the dorsal and ventral roots do not join peripherally
as they do in fishes.

---

[1] According to TRETJAKOFF the first dorsal root of Amphioxus may
correspond to the small sensory nerve occasionally occurring in the mesen-
cephalon of Ammocoetes and in the tweenbrain of birds. This very incon-
stant n. mesencephalicus or n. thalamicus may, however, in my opinion
be as well a local remnant of the ophthalmic root of the trigeminus.

THE NERVOUS SYSTEM OF VERTEBRATES.

The central nervous system of vertebrates lies on the chorda, which developes from the intestinal canal. Only the prosencephalon extends beyond it. Infolding from the dorsal ectoderm the neural tube usually first closes in the midst. This closure progressing frontally
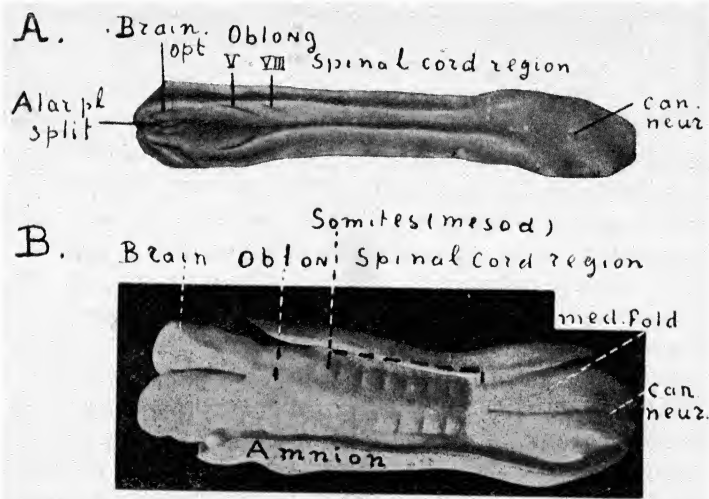
Fig. 43. A cat embryo of four somites after VON SCHULTE and TILNEY. The medullary fold is nowhere closed but narrowest in the upper spinal cord region. — B. Human embryo of eight somites after D'ETERNOD. The medullary fold is closed in the upper spinal and oblongata region. The fold is still open in the region of the prosencephalon and mesencephalon, and in the lower spinal cord.

and caudally, the open communications with the ectoderm (transitional neuropori, fig 43, B) shift more and more to the front and hindpole of the tube, where the final closure occurs (neuroporus anterior and posterior).

On the inner side of the spinal medullary tube a sulcus developes, generally poorly indicated, but of great importance, *the sulcus limitans of* HIS (see fig. 44 and 45).

This sulcus divides the spinal cord into an *alar plate,* dorsally connected secondarily with its companion of the opposite side by the
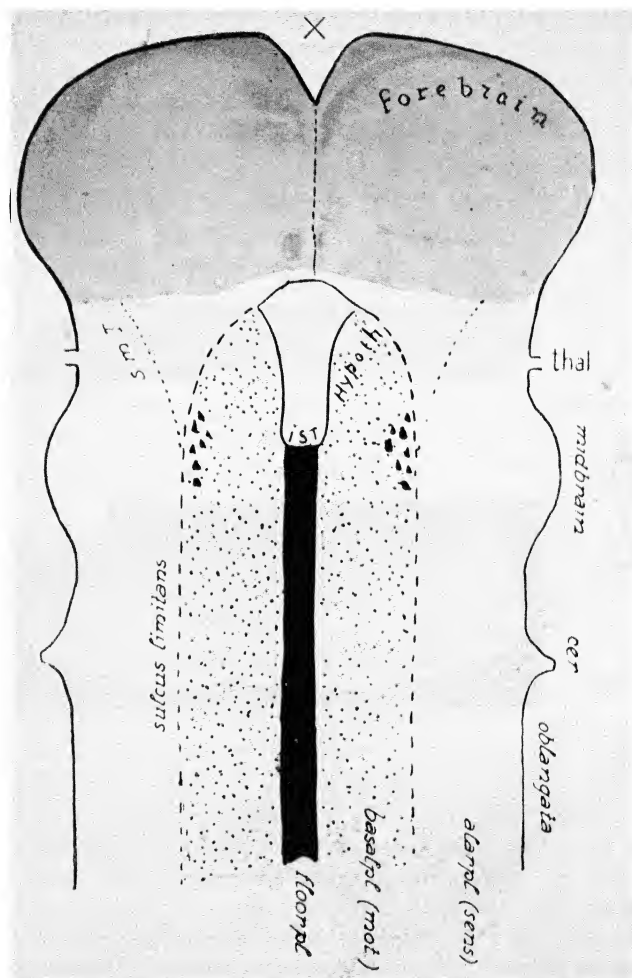
Fig. 44. Schematic representation of the different frontal extensions of the floor plate, basal plate and alar plate. The mesial dotted line in the forebrain division of the alar plates indicates the lamina terminalis, the lateral dotted lines (S. M. T.) indicate the sulcus medius thalami.

roofplate, and a *basal plate*, ab origine connected with the opposite by the floor plate (fig. 44).

Whereas the connecting floor plate terminates at the level of the isthmus (KINGSBURY, BURR), the basal plate and its dorsal border, the sulcus limitans, grow further frontally, extending to the place. where later the optic chiasm is found [1] (fig. 45). The *alar plates* extend still further, and from their frontal part the optic vesicles and forebrain develop. The frontal closure of the forebrain, occurs at the mesial dotted line in fig. 44, and forms the *lamina terminalis*.

The total coalescence of the alar plates may precede that of the basal plates. (Selachia, Amphibia, Birds). The neuroporus anterior then lies between the latter (v. WIJHE). If the basal plates coalesce first the neuroporus ant. lies between the alar plates (at ×, fig. 44). This was observed in Macrupus ruficollis by J. P. HILL, and in man by VAN DEN BROEK and others.

It is important to know these relations, since they run parallel with functional divisions (HIS, JOHNSTON, HERRICK), the alar plate being sensory and correlative, the basal plate efferent-coordinative.

The course and frontal termination of the sulcus limitans, near the optic chiasm, is important because this sulcus indicates the region of the central autonomic nuclei. In the spinal cord these praeganglionic autonomic centers are represented by the intermedio-lateral nucleus, in the oblongata by cells of the XII, X, IX and VII, in the midbrain by the motor cell groups of EDINGER and WESTPHAL which innervate the inner musculature of the eye. Finally, near the chiasm, cells occur which influence hypophysial secretion, bloodpressure and dilatation of the eye [2], the latter by means of the 1st thoracic segment.

The *N. terminalis* in many animals (fishes and Amphibia), in addition to sensory components, cointains also sympathetic postganglionic cells (BROOKOVER, MC KIBBEN). Its connection with the *praeoptic magnocellular nucleus* (n. pr. fig. 53) may also be advanced in favor of the autonomic character of this region (cf. also fig. 47).

From this it is obvious that along the s. limitans the centers of the autonomic system are located. Their cells, if they are root cells are called *praeganglionic cells*, as they do not end in effectors, but in *peripheral motor ganglia* or *plexuses* innervating viscera.

---

[1] HIS, JOHNSTON and BAILEY. According to von SCHULTE, TILNEY and KINGSBURY the basal plate extends only a short distance beyond the floor plate.

[2] KARPLUS und KREIDL. Gehirn und Sympathicus, Pflügers Archiv, Bnd. 129, 135 and 143, 1909, 1910 and 1911.
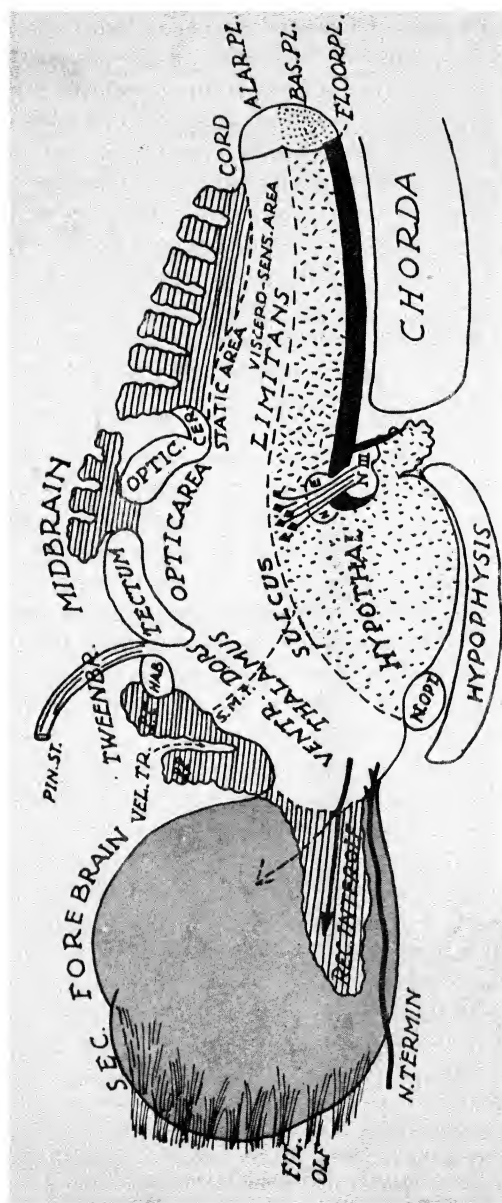
Fig. 45. Morphological divisions in a hypothetic lamprey like fish (cf. fig. 44). Only the right hemisphere is drawn. Membranous parts of the roof plate are striped. — (Only PETROMYZON has a partly choroidal midbrain roof, but the N. terminalis and the infundibular organ, drawn in this figure, do not occur in Petromyzon). P.C. = Parencephalon; vel. tr. = velum transversum; P.P. = paraphysis; pin. st. = stalks of the parietal eyes.

Phylogeny of the peripheral autonomic system.

As was mentioned in the first chapters, the peripheral plexuses, which may arise from the ectoderm as well as from the entoderm, are the only constituents of the nervous system in Coelenterates, and are still very conspicuous in Vermes, specially in the lower ones, and in Echinoderms, where they serve somatic (locomotor) as well as visceral functions,

In Molluscs the locomotor plexuses are specially developed in the foot, mantle and brachia, less so in other places. They act largely locally, partly under control of the central system (p. 50, 51). In Arthropods the somatic plexus has diminished, and somatic movements are directly under control of the central nervous system.

In the viscera of all invertebrates, however, such plexuses remain.

In the *Nemertini* the visceral plexus is confined to fibers arising from the cerebral and paraoesophageal ganglia. They spread over the larger part of the gut that also contains primitive ganglion cells (APATHY, BÜRGER 1. c.). In most Annelids a similar condition obtains (ASCOLI[1]), SANCHEZ[2]), fig. 46). In some higher Annelids in addition to this *anterior intestinal plexus* a *posterior intestinal plexus* occurs, arising from the most caudal ventral cord ganglion (see p. 37), and innervating the posterior part of the intestine (PLATE 1. c. p. 415). On the whole gut of Annelids primitive ganglioncells are seen (APATHY 1. c.).

In *Arthropods* both the anterior (cerebral) and posterior (caudal) sympathetic system are very conspicuous (red in fig. 46). The *R. intestinalis anterior* (see fig. 46) arises from the tritocerebrum and the paraoesophageal ganglia and innervates the oesophagus, stomach, heart[3]) and hepato-pancreatic gland (KEIM, ORLOW), partly directly, partly indirectly. The *R. intestinalis posterior* arises from the most caudal ventral cord ganglion (KROHN, ALEXANDRO-WICZ, 1. c.), and ends with a caudal branch on the "rectum" and with two frontal branches on the whole intestinum behind the stomach, innervating the intestinal musculature of this part.

---

[1]) ASCOLI. Zur Neurologie der Hirudineen Zool. Jahrbücher, Abt. f. Anat. und Ontogenie der Tiere, Bnd. **31**, **1911.**

[2]) SANCHEZ, El sistema nervioso de los hirudineos. Trabajos del laboratorio de investigaciones biologicas de Madrid. Tomo VII, 1909.

[3]) After JOLYET and VIALLANES, CONNANT and CLARKE the heart nerves arises from te thoracic ganglion (cf. CARLSON, Biol. Bull. Vol. VIII, 1905).

Besides on the wall of the whole intestinal tract of Arthropods bipolar and multipolar ganglion cells are found, the former being sensory cells of the mucosa, ending, according to ALEXANDROWICZ, in the intestinal muscles and thus transmitting *peripheral* reflexes. They more probably end in the caudal abdominal and paraoesophageal ganglia (ORLOV) establishing *central* reflex arcs. *From the intermediate part of the ventral cord between the paraoesophageal and caudal abdominal ganglion no sympathetic fibers arise in Astacus.*

In Limulus and Insects the intestines have a double innervation (PATTEN and REDENBAUGH). The *heart* however has a parasympathetic and sympathetic innervation (from the intermediate ganglia) already in Decapods and Insects (JOLYET and VIALLANES, CARLSON, ALEXANDROWICZ).

The confinement of the origin of the intestinal plexuses of these animals to the cerebral and caudal part of the central nervous system strongly suggests an analogy with the *parasympathetic system* of *vertebrates* (see below), the more so as also in the lowest, reduced Cyclostome, *Myxine,* no sympathetic fibers arise from the spinal, not even from the caudo-spinal system (BRANDT [1])), so that, as in most worms, only the cerebral (vagus) plexus is present, which in this animal extends to the anus. In *Petromyzon,* however, TRETJAKOFF [2]) found, in addition to the cerebral (vagal) plexus sympathetic, fibers arising from the whole spinal cord. The most caudal (preanal) region, receives its (parasympathetic) fibers from the caudal cord as it does in mammals. They are connected with the ventral, but especially with the dorsal spinal roots.

Bipolar and tripolar ganglion cells lie in the wall of the gut.

Other cells, described by JULIN as sympathetic cells in this animal, belong to the adrenals (GIACOMINI, TRETJAKOFF).

Similar observations are made in *Plagiostomes* by E. MULLER [3]), who, in addition to frontal (vagal) and caudal (sacral) parasympathetic plexuses found sympathetic fibers arising from the intermediate cord by means of the ventral and dorsal roots.

Also here sensory and motor cells occur in the wall of the in-

---

[1]) BRANDT. Das Darmnervensystem von Myxine glutinosa Zeitschr. f. Anat. und Entwickl. Bnd. 65, 1922.

[2]) TRETJAKOFF. Das periphere Nervensystem des Flussneunauges. Zeitschr. für wissenschaftliche Zoologie, Bnd. 129, 1927.

[3]) E. MULLER. Beiträge zur Kenntnis des autonomen Nervensystem I Ueber die Entwicklung des Sympathicus und des Vagus bei den Selachiern. Arch. f. mikrosk. Anatomie, Bnd. 94, 1920.

testinum and according to this author they belong as well to the cerebral as to the spinal sympathetic system.

The presence of sensory peripheral cells is doubted in Mammals.

My supposition that the cerebral and caudal rami intestinales of Astacus are to be compared with the cranial and sacral parasympathetic system of vertebrates (red in fig. 47), while the intermediate or thoraco-lumbar sympathetic system (black in fig. 47), is a new addition, is confirmed by the fact that the thoraco-lumbar system in vertebrates develops ontogenetically later than the parasympathetic system (of the head especially).

In the higher vertebrates, however, nearly all visceral organs, not only the heart, receive parasympathetic as well as interme-diate or sympathetic fibers so that apparently these two parts of the *autonomic nervous system* overlap each other.

In *mammals* the *sympathetic system* s. str., is connected with the ventral thoraco-lumbar roots[1]). Orally and caudally from this the cranial and sacral *parasympathetic system* occurs (GASKELL, LANGLEY). The effectory part of both consists of praeganglionic neurones and peripheral or postganglionic neurones.

In addition to this *primitive ganglion cells* may occur (p. 91).

The *praeganglionic* neurones of both, sympathetic and parasym-pathetic system lie in the central nervous system (see p. 81). The *postganglionic cells* of the sympathetic system are mostly aggregated in the *vertebral ganglia* [2]) and *prevertebral ganglia*, those of the parasym-pathetic system in still *more peripheral ganglia* or plexuses such as the *intramural plexuses* of AUERBACH in the stomach and gut, REMARK's, BIDDER's and LUDWIGS ganglia in the heart, the intraglandular ganglia of the salivary and other glands, the intramural ganglia of the bladder, the juxtamural ganglia of the sexual organs [3]).

For the bloodvessels, glands and unstriped muscles of the *skin* the post-ganglionic neurites arise mostly from the vertebral ganglia of the *sympathetic chain*, from the g. cervicale superius for the skin of head and neck, from the g. stellatum for the arm plexus, from the g. thoraco-lumbales for the skin of the trunk and lower extremities. Their fibers join the cutaneous nerves.

---

[1]) In man also the 8th cervical root contains praeganglionic sympathetic fibers and to my opinion the praeganglionic fibers of the hypoglossus are sympathetic.

[2]) The chainlike connection of these ganglia commences in higher fishes.

[3]) This however in not an absolute law. The medulla of the adrenal glands contains postganglionic sympathetic cells, which have the same origin as the adrenal medulla itself, arising from the thoracic neural crest (spinal ganglia).

Other postganglionic fibers of the chain ganglia end in the sarcoplasm of striated muscles (BOEKE [1]), DE BOER, AGDUHR). The sympathetic character of these amyelinated fibers is contested by HINSEY [2]), but confirmed by COATS and TIEGS [3]).

Postganglionic sympathetic fibers for the viscera originate mostly in prevertebral ganglia (g. coeliacum, g. mesentericum and hypogastric plexus).

The fact that the praeganglionic *parasympathic* fibers have their postganglionic synapses largely in intramural or intraglandular ganglia of the organs they influence may be due to the fact that the parasympathetic has little, if anything to do with the innervation of the widely spread blood vessels, but with the more localized innervation of unstriped visceral musculature, heart and glands.

In man all the regions, however, supplied by the parasympathetic system also receive fibers from the sympathetic system [4]) (see fig. 47) *and it seems that these two systems counterbalance each others functions.* So the midbrain parasympathetic (III), whose postganglionic cells lie in the ciliary ganglion causes constriction of the iris, the (1st) thoracic sympathetic, whose postganglionic cells lie in the superior cervical ganglion, causes dilalation of the iris. The bulbar parasympathetic (X) causes constriction of the bronchi, the sympathetic (Thor. 1—3) dilalation. The bulbar (X) innervation of the heart inhibits its action, the sympathetic (C. 8, D 1—3) accelerates it. Even the glomus caroticum, an internal gland with chromaffin cells, like the adrenal, receives parasympathetic (IX) and sympathetic fibers (g. cerv. superius; DE CASTRO). Similarly the sympathetic and parasympathetic innervation of the gut, abdominal glands and bladder, act antagonistically, the parasympathetic mostly stimulating, the sympathetic inhibiting the functions.

Moreover, the susceptibility of the parasympathetic and sympathetic system to drugs is different. The parasympathetic is very sensitive to atropin and pilocarpine, the sympathetic to adrenaline, which is itself a product of sympathetic cells, originating in the medullar cells of the suprarenal gland and probably also in other central and peripheral chromaffine cells of the sympathetic system [5]).

[1]) Jahrbuch f. Morphologie und mikrosk. Anatomie, Zweite Abt. Bnd 8, 1927.

[2]) Journ. of Comparative Neurology, Vol. 44, 1927.

[3]) Australian Journal of exper. Biology and medic. Science, Vol. V, part 1.

[4]) Not all the regions supplied by sympathetic fibers, however, have an additional parasympathetic innervation. So the glands, bloodvessels and pilomotor muscles of the skin do not receive a parasympathetic innervation nor does the ureter, as far as is known.

[5]) The chromaffine substance is the generator of adrenaline (GASKELL JR., MULON, STÖRK, V. HABERER).
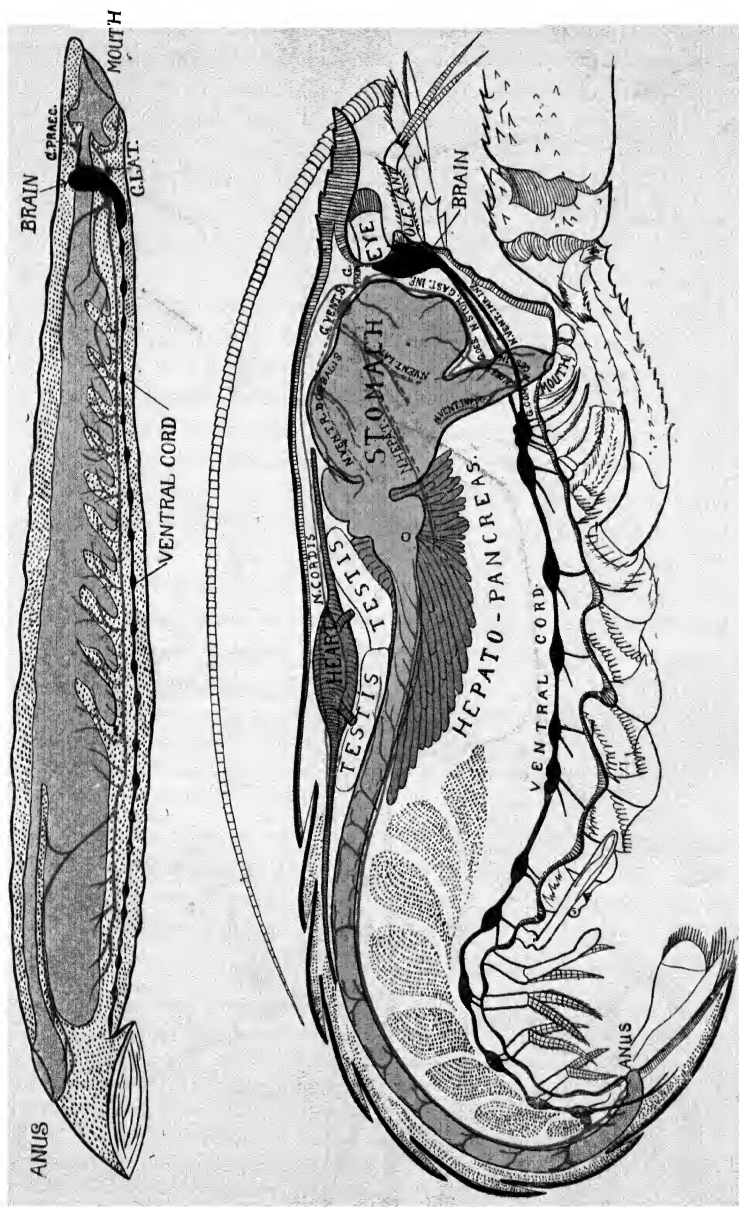
Fig. 46. Intestinal innervation in an Annelid (Hirudo) and in a lobster (Astacus). In Hirudo all the intestinal fibers come from prae-cerebral, cerebral and paraoesophageal ganglia. in Astacus also from the last abdominal ganglion.
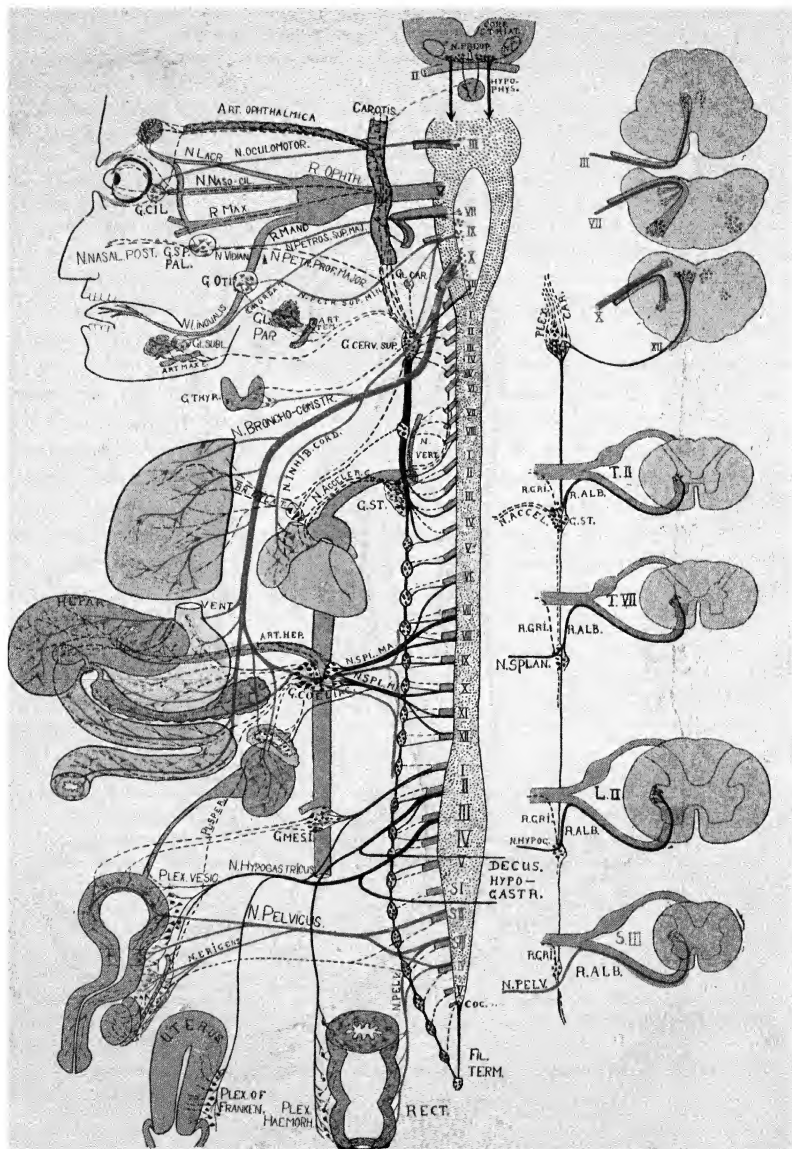
Fig. 47. Scheme of the human autonomic nervous system, chiefly after L. R. Müller, the vagus after Iwama. Sympathetic system black, parasympathetic red. Praeganglionic fibers full, postganglionic dotted.

The *ontogenetic origin of the postganglionic autonomic cells* is very remarkable from the viewpoint of neurobiotaxis. To understand this, we must realize that the viscera contain relatively few sensory fibers [1]) and those that occur convey only protopathic or *dyscritic* impulses. In the stomach and intestines not even a tactile sensibility is observed in normal circumstances (LANGLEY).

Nearly all sensory fibers originate in the spinal and cranial ganglia, as do the somato-sensory fibers. Perhaps some of them arise in more peripheral cells (E. MULLER), but the neurites of these cells also probably run to the central nervous system, though they may give collaterals to the sensory spinal ganglion cells.

It is evident that these few afferent fibers of the autonomic system can give rise to only few reflexes, so that the impulses reaching the peripheral motor autonomic cells via the central reflex arc (even including the impulses from higher cerebral centres) are few in comparison to the widely ranging action of the motor autonomic system.

Most reflexes in the autonomic nervous system do not run over the central reflex arc of the afferent and preganglionic neurones, but occur as *axon reflexes* (LANGLEY) of postganglionic neurites [2]). This means that an impulse caused by the stretching of an unstriped muscle ascends along the axons of the postganglionic neurones.

The ambiconductive character of axons (see p. 7) enables such *antidromic reflexes*, even in somatomotor neurites as appears from KüHNE's experiment on the halved m. gracilis of the frog. The upper and lower parts of this muscle are innervated by dichotomizing branches of one nerve and if one branch is stimulated peripherally, both halves contract (SCHILF).

Ascending along the neurite the impulse reaches the postganglionic cell but cannot continue in the praeganglionic fiber as there is a synaps. So the impulse flows off sideways through collaterals to other parts of the effector or to primitive ganglion cells.

As the cellbody of a neurone always shifts in the direction whence

[1]) In the spinal rami communicantes albi, through which the pra ganglionic and sensory sympathetic fibers run, the relation between the motor and sensory fibers varies from 10/1 to 4/1 (RANSON). Moreover the postganglionic motor cells are certainly a thousand times more numerous than the praeganglionic, while the sensory fibers hardly increase peripherally. From this appears how poor the sensory innervation is, compared to the motor.

[2]) Also in the praeganglionic system axon reflexes may occur as was experimentally proved by SOKOWNIN, LANGLEY, but probably they rarely occur physiologically, on account of the synaptic condition in the peripheral ganglia.

the majority of impulses come, it may be expected on account of the axon reflex that in the autonomic nervous system the postganglionic cells (and only these) shift in the direction of the axon, thus approaching the effector.

Now this really occurs. The postganglionic neurones of the spinal autonomic system originate from the spinal neural crest [1]). Keeping near the bloodvessels [2]), (HIS JR.) they shift peripherally in the direction of their effectors, i. e. in the direction of their axones, — which develop in this period of migration (STREETER).
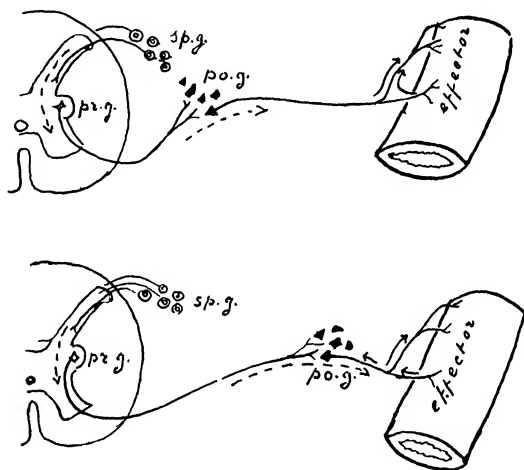
Fig. 48. Scheme of the development of postganglionic sympathetic cells (po. g.) from the same primordium as the spinal ganglion cells (sp. g.) and their neurobiotactic migration as a consequence of the postganglionic axon reflex (full drawn arrow). The central reflex arc over the spinal ganglion cells and praeganglionic sympathetic cells (pr. g.), indicated by a dotted arrow, is less used. The peripheral dendrites of the spinal ganglion cells are not drawn.

The migration path of the postganglionic cells of the cranial parasympathetic is from the cranial neural crest along peripheral fibers

---

[1]) This is proved by E. MULLER and INGVAR and by H. S. BURR, who found that embryos of Amphibia and chicken in which the neural crest s removed develop no postganglionic neurons at all. KUNTZ, however (Journ. of Comp. Neur., Vol. 32, 34, 1920 1922) believes that some postganglionic cells migrate along the ventral roots.

[2]) The bloodvessels are a part of their effectors.

of the cranial nerves. Thus the postganglionic cells of the ciliary ganglion shift along the III and upper V branch and the postganglionic cells of the sphenopalatine, sublingual and otic ganglion, arising from from the neural crest of the Vth shift along the 2d and 3d V branch, the intramural heart ganglia and those of AUERBACH's and MEISSNER's plexus, from the stomach to the ileo-coecal value, along the vagus.

The presence of primitive ganglion cells in the plexus of MEISSNER and AUERBACH (CAJAL) is denied by G. C. HUBER and C. HILL, who also doubt that plexus cells arise from the *entoderm* as was concluded by TELLO, who found them in the wall of the gut before the vagus has reached that part of the intestine (chick).

The peripheral shifting of the sympathetic and parasympathetic *postganglionic* cells [1]) is consequently a result of the neurobiotactic influence of the axon reflex, while an origin of enteric plexus cells from the entoderm, *if confirmed*, would show that plexuses of entodermal origin, so abundant in invertebrates, may still occur in birds. It is further interesting that the rate of conduction in the enteric plexus, according to ALVAREZ, is no more than that in the primitive plexus in Coelenterates (20 cm. per second).

A difference with the peripheral somatic plexuses of invertebrates is established by the fact that the autonomic nervous system of vertebrates does not contain sensory nerve fibers ending in peripheral ganglia (HUBER [2]) and HILL [3])), as frequently occurs, with neuro-sensory cells especially, in the local somatic plexuses of lower invertebrates.

The absence of local sensory reflex arcs in the gut may result from the fact that the mucosa, though very sensitive to chemical stimulation and tension, has no important tactile sensibility. Whereas

---

[1]) This explanation involves that the postganglionic cell is not connected synaptically with a third neurone, but directly with an effector, as is true.

[2]) G. C. HUBER. Lectures on the sympathetic nervous system, Journ. of Comp. Neur. Vol. VII. 1907, and The morphology of the sympathetic system. Report of the XVII international Congres of Medicine, London, 1913. It is also denied by LANGLEY, who has the greatest physiological experience on this subject. For Crustacea this is also doubted (ORLOV, cf. p. 84).

Endings in the spinal ganglia, however, may occur (DOGIEL, HUBER) and explain the clinical phenomenon of "referred pain" (HEAD).

[3]) In the myenteric plexus, however, association cells occur, linking up different motor cells (C. HILL, A contribution to our knowledge of the enteric plexuses Phil. Transactions Roy. Soc., London, Ser. B. Vol. 215, p. 355).

the skin and also the entoderm of Medusae, is exposed to a great variety of impulses and thus develops a great sensitiveness, the intestinal tract of vertebrates is only passed by substances whose consistancy is in accordance with the mucosa and the further conveyance of which is the chief function of the motor autonomic system.

Cyclostomes.

The Cyclostomes show the full prototype of a vertebrate brain.

The *prosencephalon* is differentiated here into two parts, the secondary forebrain or *telencephalon*, and the *tweenbrain* or *diencephalon*. The *telencephalon* is paired, its development being due to the neurobiotactic influence of paired [1]) olfactory placodes (cf. p. 96).

The *deuterencephalon* is differentiated into a *midbrain* and *oblongata*, both provided with a highly protruding choroid which (see fig. 45 and fig. 95), is separated by the solid hind wall of the midbrain, and the cerebellar plate. This differentiation of the deuterencephalon into two parts is due to the development of the eyes, the optic tracts ending in the midbrain roof, in front of and behind the midbrain choroid, whereas the dorso-lateral wall of the oblongata is chiefly concerned with lateral line and static impulses in addition to touch (V) and taste (VII, IX and X).

The central canal widens in the oblongata forming the *fourth* or *rhomboid ventricle*, covered by a small cerebellum (cer. pl.) and the large choroid. The lateral extension of this ventricle, not yet occuring in this form in Amphioxus, is due to the enormous increase of dorsal sensory roots in this region: the trigeminus and the nerves of the lateral line organs of the head and body and the nerve of the labyrinth (VIII).

At the entrance of these nerves (fig. 49) the oblongata attains its greatest width.

The increase of general and specialized dorsal root fibers in this region causes the dorsal part of the oblongata to receive a great many sensory stimuli, which apparently cause its dorsal walls to grow outward, instead of coalescing with each other in the midline.

In the lumbo-sacral region of the spinal cord of birds at the level of the sciatic nerve roots, a similar process occurs, but only secundarily, when the

------

[1]) An intermediate placode is also present. It continues backward in the primordium of Rathke's sac, from which the larger part of the hypophysis arises. In higher animals it disappears, forming the „Vorraum" of the hypophysis (WOERDEMAN).

central canal has already closed. So only the posterior funiculi and posterior horns are drawn apart, the gap being filled with cells containing glycogen (glia, TERNI; pia cells, PRUSS, KAPPERS).

Behind these roots enter the real branchial nerves (VII, IX, X), which, in addition to some *cutaneous* branches (JOHNSTON), carry mostly *general visceral* and *taste* fibers.

The *spinal cord*, rather flat in Petromyzon (fig. 50, 100), shows a higher differentiation by the development of many nerve cells. This *gray substance* extends on both sides of the central canal as a single pair of wings, not as two pairs, a dorsal and a ventral one, as in higher vertebrates.

In its roots primitive conditions prevail, the sensory and motor roots not joining but emerging alternatingly. Both, the dorsal and ventral roots contain sympathetic fibers (cf. p. 84). The somato-sensory fibers arise partly from intra-medullary cells (fig. 50), largely from spinal ganglia. The segments of the cord and the different parts of the central nervous system are inter-related by fiber tracts, establishing correlations of impulses for coordinate movements. Thus the *forebrain*, though largely olfactory, receives tertiary visceral fibers from the ventral tweenbrain (JOHNSTON), while it sends tertiary olfactory fibers to the dorsal and ventral part of the latter.

The dorsal connection with the diencephalon ends in the *ganglia habenulae*, the ventral one in the *hypothalamus*, which are the most developed regions of the diencephalon in Petromyzon (cf. fig. 45).
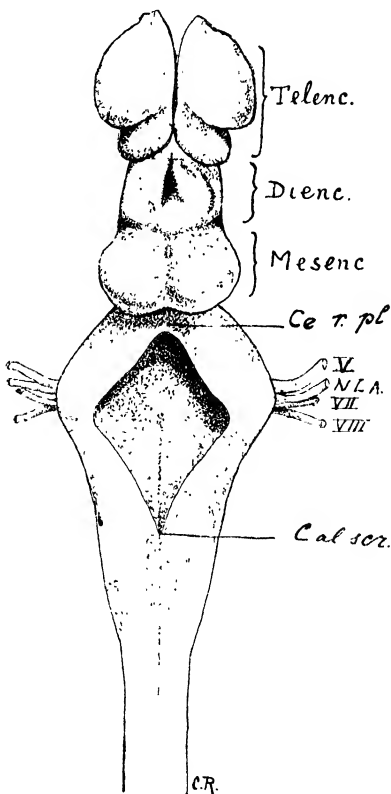
Fig. 49. Dorsal aspect of the brain of PETROMYZON. The greatest width of the fourth ventricle corresponds with the entrance of the V, VII, VIII and lateralis anterior roots.

The *ganglia habenulae*, of which the right one is larger than the left, also receive neurites of the large pineal and parapineal eyes. Fibers from these ganglia run to an efferent center, located at the frontal midbrain base: the *nucleus interpeduncularis* (N. E., fig. 45), from which, as from the hypothalamus, efferent impulses run to the motor nuclei of the mouth and gills, and, by intercalated neurones, to the motor centers of the spinal cord. It thus appears that the ganglia habenulae (or epithalamus), hypothalamus and interpeduncular nucleus are important centers for centrifugal olfactory reflexes. The hypothalamus, moreover may receive fibers from
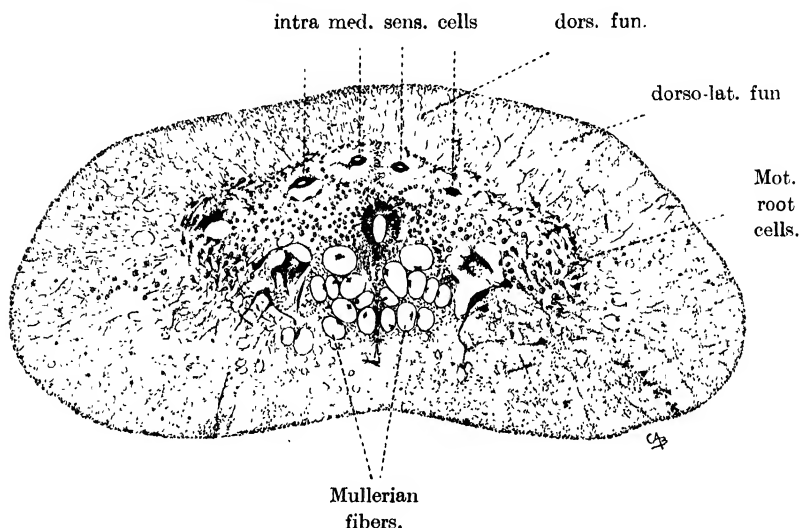
Fig. 50. Transverse section of the cervical cord of PETROMYZON fluv. (cf. also fig. 100).

the sensory mouth centers, so that the ventral part of the thalamus is a correlation center for the exploration of food.

In addition the hypothalamus has a function in regard to metabolism, as is not only expressed by the presence of the hypophysis, but also by the praeoptic sympathetic nucleus which innervates the hypohysis (JOHNSTON).

Whereas the correlations of the ventral thalamus are chiefly visceral, those between the *midbrain, cerebellum* and *oblongata* are entirely somatic and serve locomotion.

As already in invertebrates (p. 22 and 45) optic and static impulses are often correlated, similarly in Petromyzon the optic midbrain

roof and the static area of the oblongata (including the cerebellum) are closely interrelated, both subserving orientation in space. From both regions important descending reflex tracts: tectobulbar and descending cerebellar and vestibular fibers arise, influencing the position of the eyes and body. In addition the large *Mullerian fibers* (fig. 50, 100) occur, resembling the neurochords of Annelids, Crustacea, and the giant fibers of Amphioxus, with the difference that they elaborate chiefly static stimuli, correlated with visual and trigeminal impulses and only run in a caudal direction.

Another difference is that they do not decussate (TRETJAKOFF).

The fact that such large reflectory paths only originate in the midbrain and oblongata, and not in the caudal region of the cord, as occurs in Annelids and in Amphioxus, demonstrates *the greater predominance of the frontal part of the nervous system*, a feature that becomes more and more evident in higher vertebrates.

For the motor nuclei of the midbrain and oblongata I refer to figure 67 and page 106 and 107 where their arrangement is compared with the topography of these nuclei in Plagiostomes and Teleosts.

Plagio'stomes.

The nervous system of Plagiostomes, though built according the same principles as that of Cyclostomes, shows a further differentiation in all regions.

The forebrain is much larger. In the tweenbrain the ventral thalamus, but especially the hypothalamus, is considerably increased. The latter has developed large lobi laterales and possesses, in addition to the hypophysis, a large *saccus vasculosus*, containing the *infundibular sense organ* (lacking in Cyclostomes). Moreover, the midbrain roof, still partly choroidal in Petromyzon, has become entirely nervous.

The most striking feature of the oblongata is the enlargement of the static area by the formation of a special center for the dorsal root of the lateral nerve of the head (l. lin. lat. anter., fig. 53), above the centre for the ventral root of this nerve. The posterior lateral line nerve (of the body) and the vestibular nerve enter the same region als the ventral root of the anterior lateral line nerve (static area, fig. 53).

The cerebellum, in particular, is considerably developed, and from a simple transverse connection between the static areas of both sides — as it is in Petromyzon — has changed into a large organ with a ventricle of its own. In the larger specimens it may

acquire enormous dimensions, being frequently folded, as in Car-
charias, fig. 54, Lamna cornubica and in the larger skates, specially
in Myliobates (VOORHOEVE).
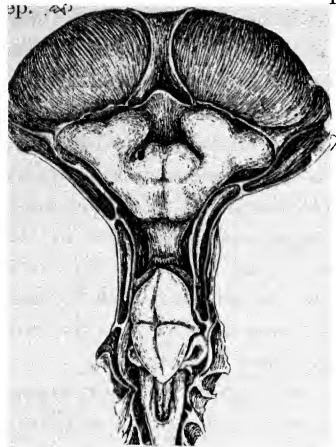
Fig. 51. The olfactory lobes of
Scyllium can., grown out to the
olfactory epithelium.

A special feature of the Selachian
forebrain are the large and some-
times very long olfactory stalks,
They give a striking contrast with
Petromyzon, where the olfactory
epithelium lies against the hemis-
pheres. These stalks terminate in a
bulbar thickening (formatio bulbaris)
behind the nasal epithelium (olf. ep.)
thus demonstrating the neurobio-
tactic influence of the paired olfac-
tory placodes on their development.

The neurobiotactic influence of the
olfactory placodes on the outgrowth of
the forebrain is experimentally confirmed
in Amphibia by BURR [1]) (cf. also WEISS-
FEILER [2]), who transplanted an olfactory
placode to another place of the head, and then
saw the hemispherical wall growing out to the
transplanted placode [3]).

These stalks are hollow, their cavities being
the direct continuation of the lateral ven-
tricles of the forebrain. Between the stalks,
the forebrain proper protrudes (see fig. 51)
equally paired. In some sharks (fig. 54) and
skates (fig. 52) the paired character, howe-
ver, is hardly indicated externally, since the
mesial hemispherical walls in these animals
coalesce.

These walls consist of a medial continua-
tion of the *pallium*, and a medial continua-

Fig. 52. Raja clavata

[1]) BURR, Some experiments on the transplantation of the olfactory placode
in Amblystoma. Journ. of Comp. Neurology, Vol. 37, 1924.

[2]) WEISSFEILER, Régénération des lobes olfactifs et des hemisphères céré-
braux chez les Batraciens urodèles. C. R. de la Soc. de Biologie, Tome 91, 1924.

[3]) The influence of the placodes appears also from the fact than in cases

tion of the base of the brain, forming the *septum*. The meeting of the pallium and septum is generally indicated by a deep furrow on the ventricular side, *fiss. septopallialis*, due to their opposed growth (cf. fig. 58).

Corresponding with this fissure in some sharks (Acanthias, Hexanchus; Young) an impair, tubelike extension of the median ventricle occurs, called lobus olfactorius impar (Rabl Rückhardt) or recessus neuroporicus [1]) (Burckhardt and v. Kupffer). It is homologous to the interhemispherical recess in cyclostomes, indicated in fig. 45 as recessus interolfactorius, and is a frontal extension of the *primary* prosencephalic ventricle, while the lateral ventricles and olfactory stalks are *secondary* or *telencephalic formations*.

Just in front of this unpaired tube in Hexanchus the paired *nervus terminalis* enters the mesial wall of the telencephalon (cf. fig. 53).

After partial crossing it terminates in the septum, some fibers passing caudo-ventrally in the direction of the praeoptic recess.

The nerv. terminalis is largest in Hexanchus, but also conspicuous in Scyllium, where it has a well defined ganglion, lying on the central end of the olfactory stalk (as indicated in fig. 53). In most other Plagiostomes its cells are scattered in the course of the nerve.

Locy has made us familiar with the course of this nerve in Selachians; where it provides the olfactory mucosa with sensory fibers, in addition to which sympathetic fibers occur (Mc Kibben). The latter, however, are more conspicuous in Teleosts and Amphibia.

The relations of the n. terminalis in sharks remind us of those found in Amphioxus, allthough the entrance of the terminal nerve in sharks is more dorsal, the basis of the forebrain having grown out dorsally as a septum.

The *telencephalon* receives a great many olfactory fibers from the mitral cells in the bulbar formation. The lateral and dorsal fibers spread over the lateral and dorsal parts of the pallium respectively with the exception of the caudal mantle part (*primordium hippocampi*, Johnston). This receives tertiary olfactory fibers, and fibers of the *tractus pallii*, a crossed, probably visceral tract originating in the midbrain and hypothalamus. Ventral olfactory fibers end near the

---

of arhinencephaly, where these placodes fail, the anterior parts of the forebrain remains unpaired. (de Jong, Riese).

[1]) This is a wrong name as it has nothing to do with the neuroporus, the final frontal closure of the Selachian brain, lying at the level of the optic recess (van Wyhe, see also p. 81).

ventral surface and in a ventricular protrusion of the lateral wall immediately behind the olfactory stalk, in front of the palaeostriatum. This protrusion may be called *epistriatum* (fig. 53).

From the forebrain two tracts arise, first studied by EDINGER. The taenia thalami·runs to the ganglia habenulae. Another one (tr. str. th.) to the hypothalamus (fig. 53). From the ganglion habenulae descending neurones (f. retr.) lead ventrocaudally to the nucl. interpeduncularis (N. i. p.) of the midbrain and from the hypothalamus to the oblongata (tr. lobo-peduncularis). These are the most important efferent paths of the forebrain. The tr. lobo-peduncularis, however, is not merely olfactory, since the hypothalamus is probably related to the touch sense of the head by secondary trigeminus fibers and perhaps also to taste.

On the level of the *foramen* MONROI lies the small *palaeo-striatum*, from which large efferent neurones enter the strio-hypothalamic peduncle. The palaeostriatum is contiguous with cells, lying in the thalamic course of the bundle (peduncular nucleus).

The forebrain is limited caudally by the *velum transversum,* a transverse fold of the choroid (fig. 53: v. t.), which protrudes dorsally in front of and behind this fold. The frontal sac is the *paraphysis,* the caudal one, which attaches to the hind wall of the habenula, the *parencephalon* [1]).

Behind this attachment the stalk of the purely glandular epiphysis is seen. Parietal eyes do not occur in Plagiostomes, though rests of neurosensory cells are occasionally found in the epiphysial stalk.

The conversion of the parietal eye into a gland is an interesting example of a nervous organ changing into a hormonistic one (like part of the hypophysis, p. 100, and the adrenal gland).

Of the gray substance of the *tweenbrain,* the dorsal part, lying above the sulcus medius thalami (fig. 45, s. m. t.) is small, but the ventral part, especially the hypothalamus, is very large. The former is represented only by the asymmetric ganglia habenulae, the left of which is the larger one in Plagiostomes, a small lateral geniculate nucleus, receiving optic collaterals, and some subhabenular gray matter.

In mammals, this relation is reversed, the dorsal part of the thalamus being the largest (see fig. 84). This is a consequence of the great number of ascending bulbo-thalamic impulses that end in the dorsal thalamus of mammals by which they are transmitted to the forebrain.

Such thalamic forebrain projections, however, do not yet occur in Plagiostomes, where efferent forebrain tracts to the hypothalamus and ventral thalamus prevail.

[1]) Or pulvinar epiphyseos, as the stalk of the epiphysis runs over it.
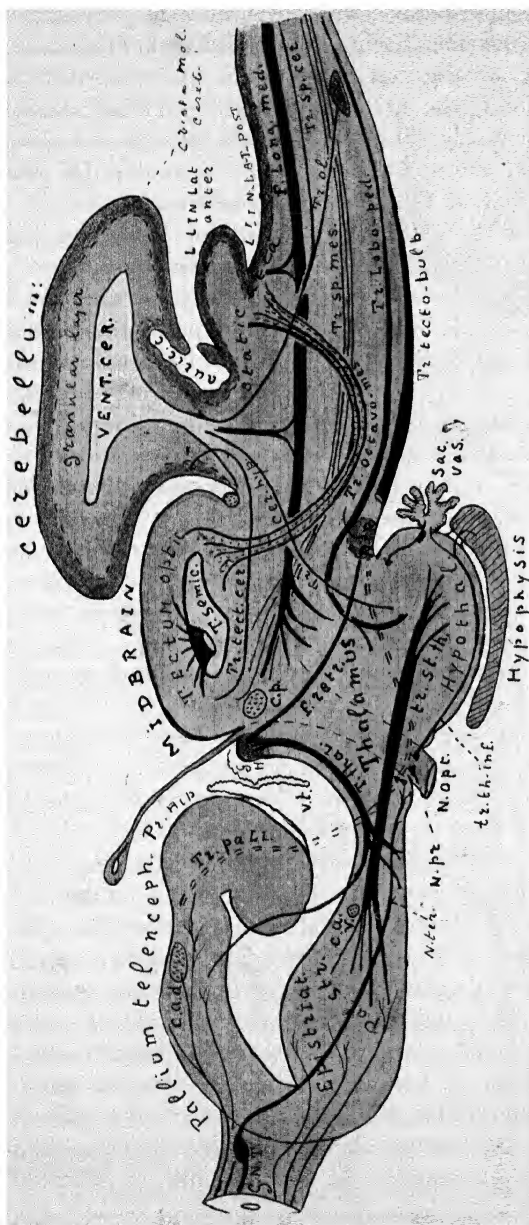
Fig. 53. Some tracts in the brain of Spinax niger.

c. a. d. = commissura anterior pars dorsalis; c. a. v. = commissura anterior pars ventralis; c. p. = commissura posterior; f. retr. = fasc. retroflexus; f. long. med. = fasc. longitudinalis medialis sive centralis; G. H. = ganglion habenulae; N. pr. = nucleus praeopticus; N. ter. = nervus terminalis; o. i. = oliva inferior; pr. hip. = primordium hippocampi; Tr. cer. hyp. = tract. cerebello-hypothalamicus (crossed); Tr. lobo-ped. = tract. lobo-peduncularis; Tr. octavo-mes. = tract. octavo-mesencephalicus or lateral fillet; Tr. ol. = tract. olivo-cerebellaris; Tr. sp. cer. = tract. spino-cerebellaris; Tr. sp. mes. = tract. spino-mesencephalicus; Tr. st. th. = tract. strio-thalamicus; Tr. tecto-bulb. = tract. tecto-bulbaris; Tr. tect. cer. = tract. tecto-cerebellaris; Tr. th. inf. = tract. thalamo-infundibularis arising in the tectum opticum); Tr. tect. cer. = tract. tecto-cerebellaris; Tr. th. inf. = tract. thalamo-infundibularis (to the hypophysis and to the bloodvessels of the saccus vasculosus); v. t. = velum transversum.

The course of the fasc. retroflexus indicates approximately the limit between the tweenbrain and midbrain in this animal. The greater size of the ventral thalamus, compared to the dorsal thalamus is obvious.

The ventral thalamus is also connected with the cerebellum, by ascending and descending fibers, which increase the importance of this area for prey hunting movements.

The *saccus vasculosus*, the neurosensory cells of which extend into the ventricle, probably subserves the perception of the depth on which the animal moves, the pressure of the ventricular fluid running parallel to that of the surrounding medium.

The bloodvessels of the saccus, which are very numerous, and also the bloodvessels and glandular cells of the hypophysis, receive a sympathetic innervation by means of the *tr. thalamo-infundibularis* (fig. 53, tr. th. inf.). — This bundle arises in the praeoptic nucleus, (n. pr.) which is richly vascularized and may also receive some endings of the terminal nerve.

The presence of this nucleus, which influences bloodpressure and hypophysary function, near the praeoptic recess proves the sympathetic character of that region, which corresponds with the frontal end of the sulcus limitans (see fig. 45).

The *hypophysis* of Plagiostomes differs from that of Cyclostomes by the fact that the intermediate olfactory placode is included in it, forming its vestibulum (Vorraum; WOERDEMAN).

This is an other example of a nervous primordium reverting into a hormonistic organ, as occurs in the epiphysis (see above) and in the medulla of the a renal gland.

The *midbrain* is very large. This is due to the large optic nerve, the fibers of which all end in the roof or *tectum*, the lateral geniculate ganglion, to which most of them go in mammals (cf. p. 151), receiving only optic collaterals in sharks.

The *tectum opticum* receives crossed secondary fibers from the cord (EDINGER's tr. spino-mesencephalicus) and area statica (tr. octavo-mesencephalicus), though the latter end mainly under the optic ventricle (WALLENBERG) in the *torus semicircularis* (t. semic. fig. 53). Thus, the dorsal part of the midbrain is a centre of somatic correlations, serving optic, static and kinaesthetic [1] orientation.

On this account it is not strange that it has an efferent connection with the cerebellum, *tr. tecto-cerebellaris*, and with the motor nuclei of the eyes and body: the crossed and uncrossed *tr. tecto-bulbaris*. Underneath the tectum, in the *tegmentum*, the *fasciculus longitudinalis centralis* or *medialis* (fig. 53) originates, an effectory

[1] The mesencephalic trigeminus root has proprioceptive functions (WILLEMS).

coordinating system which has contro-lateral relations by means of the *posterior commissure* (c. p.) and which is enlarged in the oblongata by fibers from the cere-bellum and from the static area (fig. 54, fasc. long, c.).

The importance of the midbrain as a somato-motor centre also appears from the fact that electric stimulation causes cros-sed and uncrossed move-ments of the eyes, body and tail [1]).

The *cerebellum* consists of an unpaired middle part or *corpus* and paired *auriculi* (fig. 54). The latter are the direct con-tinuation of the static area of the bulb, which is itself covered by a con-tinuation of the *crista cerebellaris (pars bulbaris cerebelli,* TILNEY). The auriculi receive nothing but primary and secon-dary fibers from the static nerves (N. vestibu-laris and N. N. laterales).

They connect under-neath the corpus *(pars jugale,* TILNEY).

The corpus cerebelli receives fibers from the tectum (cf. p. 100), the
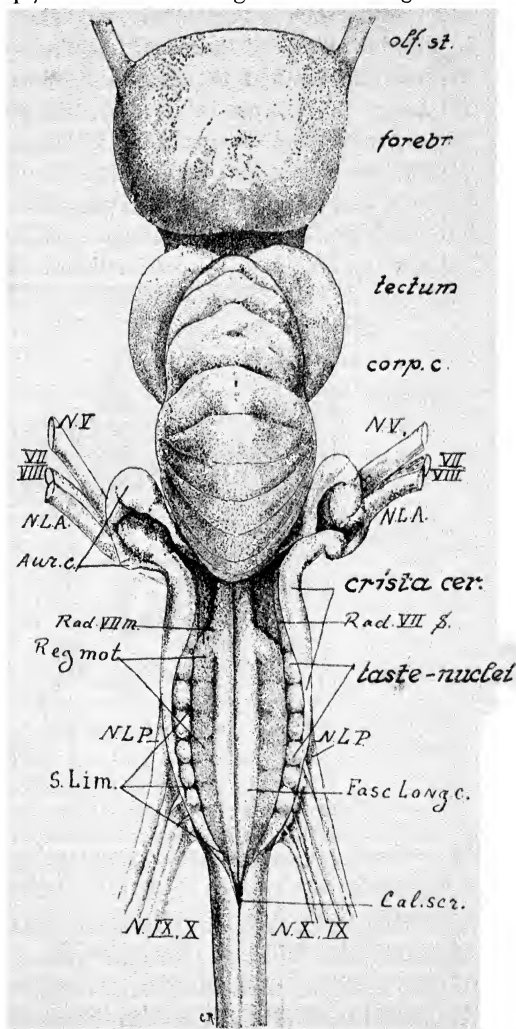
Fig. 54. Dorsal aspect of the brain of Carcharias glaucus. corp. c. = corpus cerebelli.

spinal cord (*tr. spino-cerebellaris ;* fig. 53, tr. sp. cer.) and the inferior olive (*tr. olivo-cerebellaris;* fig. 53, tr. ol.).

This difference in functional connections of the corpus and auriculi is also indicated by the fact that the auriculi are largest in those Plagiostomes in which the static nerves (especially the N. N. laterales), are large, for instance in the skate (fig. 52), while on the other hand, the corpus cerebelli increases (by folding) with the increase of body size. So the corpus cerebelli is unfolded in the small Spinax (fig. 53), has one fold only in Scyllium (fig. 51) and Raja clavata (fig. 52), but many in the large Carcharias (fig. 54).

Three layers may be distinguished in the corpus as well as in
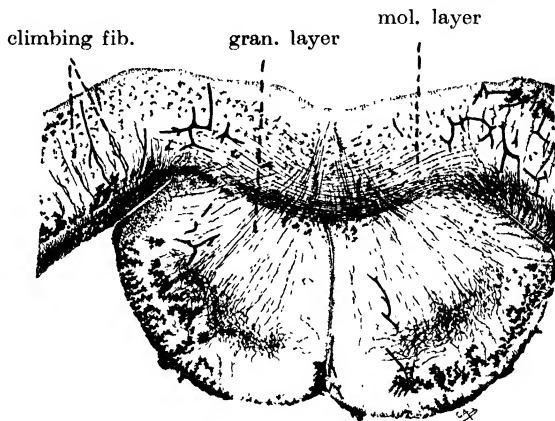
Fig. 55.   Granular layer and molecular layer
with parallel and climbing fibers in a shark.
PURKINJE cells not impregnated.
Transverse section made by DROOGLEEVER FORTUYN.

the auriculi, an external or molecular layer, the direct continuation of the crista cerebellaris oblongatae, a layer of Purkinje cells and a granular layer (see fig. 56). The connections established in these layers are the same as in mammals.

Some afferent fibers end as *moss fibers* on the *granular cells*, others as *climbing fibers* on the dendrites (and bodies) of *Purkinje cells*. These dendrites branch chiefly in the fronto-caudal *sagittal* plane [1]) of the

---

[1]) The same is observed with the dendrites of the *basket cells* in the molecular layer, the axones of which take also a sagittal course, transmitting parallel fiber impulses to various Purkinje cells.

molecular layer, perpendicular to the *parallel fibers*, a neurobiotactic consequence of the perpendicular stimulus irradiation from these fibers.

The latter are the *transversely dichotomizing* neurites of the granular cells that transmit the moss fiber impulses received by these cells to the dendrites of the Purkinje cells on both sides, the left and right side, of the cerebellum (fig. 56).

The Purkinje cells, consequently, receive two sorts of impulses, *direct* ones from climbing fibers and *indirect* ones from moss fibers, by means of the granular cells and their parallel fibers.

It has been supposed that these impulses differ in character (CAJAL),

Parallel
fibers.

Purkinje
cells.

Granular
cells.
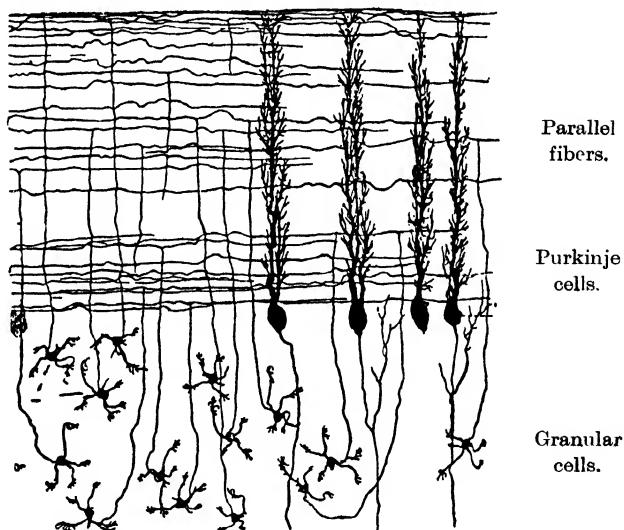
Fig. 56. Scheme of nervous transmission in the
cerebellum, after KÖLLIKER. Transverse section.

the climbing fibers being static, the parallel fibers proprioceptive, but this is not sufficiently proved. The two ways of the transmission of impulses to the Purkinje cells, which are the effector cells of the cerebellum, involves however, important conductive differences.

The transmission by means of a climbing fiber is *unilateral*, being *localized* to one or few Purkinje cells, whereas that of the moss fibers is *spread bilaterally* over the cerebellum, each parallel fiber dichotomizing left and right (fig. 56).

This double transmission is very interesting and I am inclined to think that the parallel fiber transmission acts in a complementary manner to the direct transmission, regulating its action on the Purkinje cells.

Since we know that the corpus cerebelli or vermis influences the body musculature bilaterally (cf. page 163), it does not seem impossible that this bilateral function, is influenced by the granular parallel fiber system.

The Purkinje cells are the common effectors of both the climbing and parallel fibers. In fishes (CAJAL, KAPPERS) and Amphibia (HERRICK) their neurites run to subcerebellar cells related to the vestibular nuclei. In reptiles, birds and mammals the number of these cells increases and they grow into the cerebellum (neuro-biotaxis; v. HÖEVELL), forming the dentate and fastigial nuclei, which are still failing in fishes.

Other Purkinje neurites join the fasc. longitudinalis centralis forming the direct *tr. cerebello-motorius* (KAPPERS) that ends on reticular cells of the oblongata and midbrain (perhaps also in the spinal cord).

The *cranial nerves* are more developed than in Cyclostomes.

There are three *ventral motor* [1] *roots* in the *oblongata* and *midbrain*, the hypoglossus, abducens and oculomotorius.

The *hypoglossus* is represented in sharks by two or three occipito-spinal roots, that innervate fronto-ventral trunk myotomes.

The *abducens*, originally a postotic nerve in all vertebrates, keeps its postotic position in adult Plagiostomes, its nucleus being influenced chiefly by reflexes of the VIII and lateral line nerves.

The *oculomotor* has also connections with the *ciliary plexus*, that in addition receives sensory fibers from the ram. ophthalmicus profundus V (NORRIS and HUGHES).

The *dorsal roots* of the oblongata are much larger than the corresponding roots in Petromyzon. They contain sensory and motor fibers, including praeganglionic fibers to the parasympathetic ganglia of the head. The V sends only sensory fibers to the ciliary plexus but the VII, IX and X'send praeganglionic fibers to the parasympathetic ganglia occuring on their posttrematic rami (NORRIS and HUGHES).

---

[1] The presence of proprioceptive fibers in the eye muscle nerves (including the IV) is only proved in mammals (TOZER and SHERRINGTON), but it is highly probable that they also occur in lower animals.

The sensory functions of the dorsal roots differ. The *trigeminus* is exclusively somatic, innervating the skin of the head and the ectodermal surface of the mouth in front of the pharynx. It also contains proprioceptive fibers of the jaw muscles.

The cutaneous fibers originate from the Gasserian ganglion. Entering the lateral or somatosensory area of the bulb these fibers take a caudal course to the cervical region where they associate with the endbranches of the cutaneous fibers of the spinal nerves. It is this associated function that causes its descending course, as both carry protopathic or dyscritic impulses of the skin.

Those fibers of the sensory V root that do not originate in the ganglion but from sensory cells in the tectum, the *mesencephalic sensory root*, lead proprioceptive impulses of trigeminal jaw muscles. Periphe· rally they run with the motor root (JOHNSTON, v. VALKENBURG). But also from the Gasserion ganglion some proprio ceptive fibers arise.

Whereas the trigeminus contains no viscero-sensory fibers, such fibers are in the majority in the *facial, glossopharyngeal* and *vagus* nerves.

Somato-sensory components even fail in the facial [1]) and glossopharyngeal nerves of higher Plagiostomes, only the vagus retains a somato-sensory element of importance in all vertebrates. These fibers join the descending trigeminus fibers on their way to the cervical cord (similarly as in Teleosts, see fig. 64).

This junction of the cutaneous Xth fibers with the descending Vth is another example of neurobiotaxis, both systems carrying cutaneous impulses. This also explains their ending in the upper cervical region.

The atrophy of cutaneous components in the N. VII and N. IX, already beginning in Cyclostomes, is probably due to the N. vestibularis and N. N. laterales, which may have developed from the skin components of the corresponding branchial nerves in Amphioxus. In accordance with this supposition is the fact that the fibers of the N. N. laterales and N. vestibularis enter with the facial and glossopharyngeal nerves running, however, to the somato-sensory area. The ventral root of the N. lateralis anterior enters in a frontal continuation of the nucleus of the posterior lateral nerve, while the dorsal root terminates in a separate lobe on top of this

---

[1]) Only in primitive sharks this nerve contains a small somatosensory component, which joins the descending V tract (Heptanchus, KAPPERS).

(see fig. 53). Fibers of both roots and also vestibular fibers proceed into the auricula.

The *viscero-sensory fibers* of VII, IX and X are very numerous.

A considerable part of them has become specialized in connection with the greater development of *taste buds* which are more numerous in sharks than in Cyclostomes. These taste fibers end in pearl like protrusions of the viscero-sensory region (see fig. 54). From here intercalated neurones run to the motor nuclei of the gills. Unspecialized mucosa fibers run underneath these protrusions, descending a short distance and thus forming a small longitudinal bundle, the *solitary tract*, which, however attains a much greater development in lung breathing animals, where the unspecialized viscero-sensory fibers greatly increase, while the taste fibers diminish. The whole viscero-sensory region lies medial to the somato-sensory region and keeps this position throughout its entire course in all animals (STRONG, JOHNSTON, HERRICK).

In addition the trigeminus, facialis, glossopharyngeus and vagus contain a great many *dorsal motor fibers*. These are, however, not myotomic fibers, but fibers innervating the gill- and related musculature derived from the perivisceral part of the coelomic wall (VAN WYHE). The great development of this perivisceral musculature in the head region in connection with the jaws and gills, has brought about this increase of motor components in the dorsal cranial nerves.

The trochlear nerve and nucleus also belong to the viscero-motor system (BOK), its muscle being derived from the trigeminus myomere.

The position of the *motor nuclei* in Plagiostomes is shown in fig. 67, where their arrangement is compared to the topography of the corresponding nuclei in Cyclostomes and Teleosts.

It is obvious that this arrangement differs considerably in these animals as a consequence of the different central innervation of these nuclei (neurobiotaxis).

The *oculomotor nucleus* in sharks lies entirely in a dorsal position near the fasc. longitudinalis centralis, while in Petromyzon a part of it lies near the midbrain base, another part being fused with the abducens nucleus (ADDENS).

The *trochlear nucleus* lying in the velum anticum cerebelli about the level of the trigeminus in Petromyzon has acquired a position ventral to the ventricle in sharks and moreover has shifted frontally

joining the oculomotor nucleus. On the other hand the position of the *abducens nucleus* in Petromyzon is less primitive, lying on the level of the trigeminus, its root fibers leaving directly medial to the motorroot of the latter (ADDENS [1])), together with some III rootfibers.

This more frontal position is probably due to the fact that the abducens action in the Lamprey is more intimately correlated with that of the nucleus III posterior, the oculomotor cells innervating the N. rectus inferior joining the abducens nucleus. These oculomotor fibers also leave the bulb with the abducens root in the lamprey (ADDENS).

In sharks the abducens rootlets leave the bulb between the VII and IX roots, their cells lying at the level of the vestibular root, the impulses of which strongly influence the abducens nucleus, as is also observed in mammals.

The *facial nucleus* in Petromyzon immediately follows the motor V nucleus being separated from it only by a large Mullerian cell. Both nuclei innervate the sucking apparatus of this animal. In Plagiostomes, however, the VII nucleus lies far back from the V and is connected with the motor cell column of the IX and X, subserving, as the latter do, the motility of the gill muscles.

All the cells of the VII, IX en X nuclei retain a dorsal position. This is due to the fact that the principal reflex tracts, determining the position of these cellgroups arise from the dorsal viscero-sensory nuclei and are very short only. In Teleosts, where these tracts run deeper, the topography of the V and VII nuclei changes (fig. 67).

The frontal pole of the *spino-occipital column* in Petromyzon reaches about the calamus. In sharks it extends slightly beyond it.

The *spinal cord* shows a much higher stage of development than in cyclostomes, its grey substance having differentiated into posterior and anterior horns.

The *posterior horn* is partly unpaired. Only those parts that serve vital reflexes, corresponding with the substantia gelatinosa Rolando (fig. 92 B) of higher animals (KEENAN) spread dorso-laterally by the neurobiotactic influence of the entering sensory roots, which have increased and cause their receptory cells to shift as far as the dorso-lateral periphery of the cord.

On the other hand the anterior horns, which act partly under the

[1]) The eye-muscle nerves of petromyzonts, especially in their morphological significance. Proc. Kon. Akad. v. Wetensch., Amsterdam, 1928.

influence of the posterior horns and partly under that of secondary
neurones in the ventro-lateral funiculi, never reach the ventral
periphery. Some of their dendrites extend into the posterior horns,
others into the latero-ventral funiculi unto the margin.

In adult Plagiostomes all the sensory root fibers arise from cells
in the spinal ganglia. In larvae some originate from intramedullar
transient ganglion cells (ROHON and BEARD).

Dorsal funic.

Dorsalroot

Dorsalhorn

Ventralhorn

Ventralroot
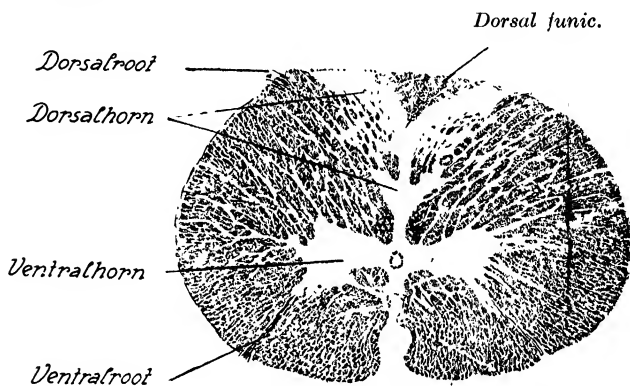
Fig. 57. Upper cervical region of the spinal cord in Galeus canis.
Chiefly the gelatinous substance of the posterior horns is
well developed. Note the small size of the posterior funiculi
(cf. fig. 93).

The somato-sensory neurites dichotomize, forming ascending and
descending bundles in the small (BROUWER) dorsal funiculi. The
viscero-sensory fibers of the dorsal roots probably end locally in the
intermediate part of the posterior horns (see fig. 57), that continues
frontally in the visceral nucleus of the comm. infima (n. comm. fig. 65)
at the calamus scriptorius (fig. 51). Praeganglionic (motor) sympa-
thetic fibers occur in the ventral as well as in the dorsal roots
(E. MULLER) but the location of their cells is not sufficiently studied.

Most of the *secondary neurones* of the spinal cord descend. Other
descending tracts enter the cord from the vestibular nuclei, running
in the ventral and ventro-lateral columns (WALLENBERG).

The most important *ascending* bundles are the crossed *spino-mesen-
cephalic* tract (EDINGER's fibers) projecting dyscritic (or protopathic)
sensibility on the midbrain, and proprio-ceptive uncrossed *spino-
olivary* and *spino-cerebellar* fibers, which ascend in the lateral funiculi.

As in Cyclostomes in the most caudal region of the cord large polynuclear gland cells are found (DAHLGREN, SPEIDELL).

Teleostomi.

The general morphology of the central nervous system of Teleostomi shows considerable differences from that of the Plagiostomes, especially in the structure of the forebrain, where very peculiar relations are found.

The teleostome forebrain can be understood only by starting with the earliest embryological development of the telencephalon from the primitive prosencephalon. The ordinary development of this telencephalon is schematically indicated in fig. 58, A, B, C.

Fig 58 A is a schematic representation of the stage in which the frontal part of the originally unpaired tube has started to widen out laterally. The pallium develops from the latero-dorsal part. From the latero-ventral part the striatum proper and a septal primordium (nucl. olfactorius medialis, HERRICK, OBENCHAIN) arise. This stage represents approximately the condition as found in Petromyzonts.

Fig. 58 B represents a stage in which both halves have developed into frontal pouches, the mesial walls of which arise by a meeting of the pallial and septal parts. This form is observed in Plagiostomes [1] and in Amphibia (B). In Reptilia (C) it only changes in so far as the striatal region grows out to a greater extent than the rest. In Mammals especially the pallium increases. In all these animals the lateral ventricles are on all sides surrounded by gray substance.

This line of development is based on the medio-ventral inversion of the pallium, which thus meets the medio-dorsally growing septum.

The development in Teleostomi is essentially different, perhaps as a consequence of the pressure of the skull in larval stages, preventing the normal outgrowth of the pallial part.

In these animals the pallial part does not increase in surface, but only in thickness. It becoms a solid mass extending laterally so that the choroid roof of the brain is considerably broadened. This condition is observed in Amia (B[1]). In more differentiated Teleosts it is even pushed ventrally, thus extending the choroid roof still more (cf. fig. 58 C[1] and 61). Another part of the pallial primordium grows over the striatum, extending unto the septum.

---

[1]) In most Plagiostomes the mesial walls of both hemispheres coalesce.

This suprastriatal part of the pallial primordium is EDINGER'S *epistriatum* It may be separated from the septum by a shallow fissure: the *sulcus limitans telencephali of Sheldon* [1]).

The larger the development of the epistriatum, the more it
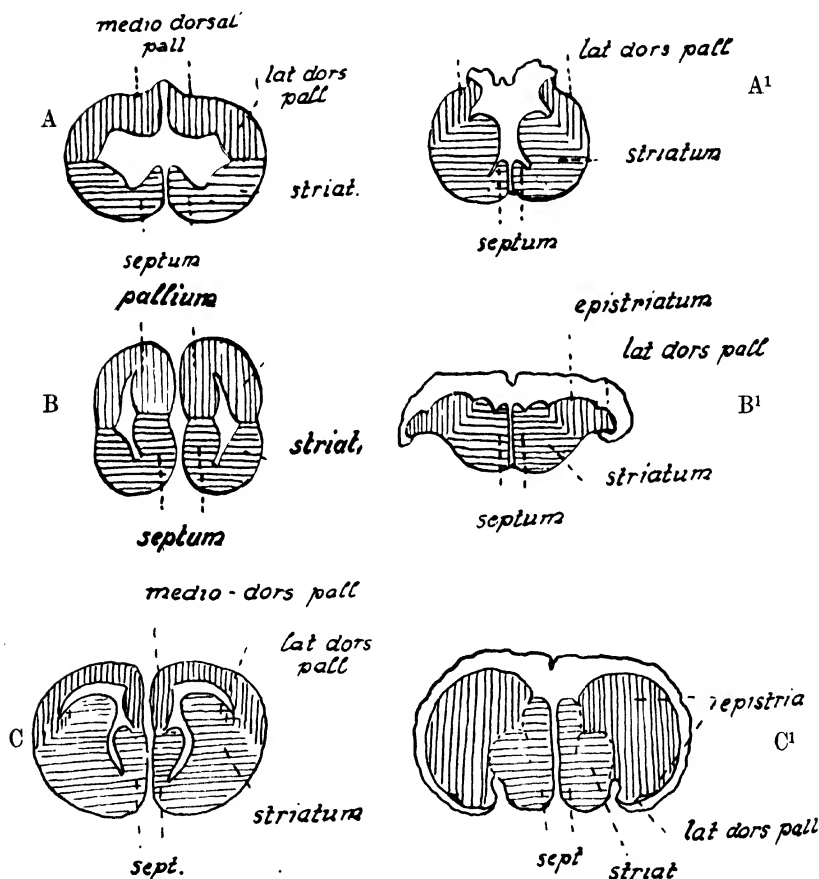
Fig. 58. Different forms of the forebrain. Petromyzon (A), Amphibia (B), Reptiles (C) and Holocephali (A[1]), Holostei (B[1]), Teleostei (C[1]).

[1]) It is evident that the S. limitans telencephali has nothing to do with the sulcus limitans of HIS, which terminates behind the forebrain. See SHELDON The olfactory tracts and centers in a Teleost. Journ. of Comp. Neur., Vol. 22. 1922.

presses the lateral pallial rudiment down, and in some Teleosts the pallial primordium even reaches more ventrally than the striatum proper (fig. 58 C[1]).

I have called this the *eversion* of the pallium. This process of eversion is first observed in the hindpart of the forebrain, where it is indicated even in Chimaera (fig. 58 A[1]). In Chondrostei, Holostei and Teleosts, however, the whole latero-dorsal portion is everted. In the Symbranchidae the eversion of the pallium attains its greatest extent (VAN DER HORST).

It is not surprising that this form of the teleostome forebrain gave many difficulties to comparative neurologists, some decades ago.

STUDNICKA and Mrs. S. PH. GAGE were the first to appreciate the proper relations, and I could confirm the exactness of this conception by showing that fiber tracts, which are located medio-dorsally in inverted brains (Cyclostomes and Plagiostomes) are found ventro-laterally in the Teleost brain.

Moreover I have observed an analogous change in the latero-dorsal wall of the oblongata, which, though inverted in most Plagiostomes is everted in Hexanchus (see fig. 59).

Fig. 59. Inversion of the lobus liniae lateralis anterioris in the oblongata of Acanthias (left) and eversion of the same region in Hexanchus (right).

I shall not deal with the exact relations of the olfactory tracts in Teleosts, so well described by SHELDON (l.c.) and HOLMGREN [1]). The everted *pallium*, the *epistriatum* and the *septum* receive most of them, and from here new neurones transmit the impulses to the habenula, ventral thalamus and hypothalamus, just as in Plagiostomes.

Apart from olfactory impulses, the *septum* receives sensory impulses from the *terminal nerve*, while ascending impressions (SHELDON) run to the septal and striatal regions from a cellgroup lying immediately behind the infundibulum, the *nucleus posterior tuberis*.

The terminal nerve, studied in Teleosts by SHELDON, BROOKOVER and N. HOLMGREN, contains also sympathetic fibers and extends to the praeoptic recess.

The *palaeo-striatum*, connected with the olfactory system by intercalated neurones only, and with ascending visceral fibers, sends out efferent fibers to the ventral thalamus and hypothalamus.

---

[1]) Zur Anatomie und Histologie des Vorderhirns der Knochenfische. Acta Zoologica, Bnd. I, 1920.

From here their impulses are transmitted to bulbar centers.

Optic or other projections from the dorsal thalamus to the forebrain are not observed in these animals, but an efferent tract runs from behind the forebrain basis to the tectum opticum (KYOZO KUDO). A similar tectal connection of the forebrain occurs in birds.

The membranous appendages [1]) of the *tweenbrain* are similar to those of sharks. The ganglia habenulae, still asymmetrical in the cartilagenous Ganoids, are practically symmetrical in most Teleosts.

The dorsal thalamus is more differentiated than in Plagiostomes.

BRICKNER [2]) pointed out that in Teleosts the *dorsal thalamus* shows an indication of an *inner thalamic segment,* a region, which increases in Amphibia and which in Reptiles, Birds and Mammals is prominent as a center of origin for forebrain projections (p. 131).
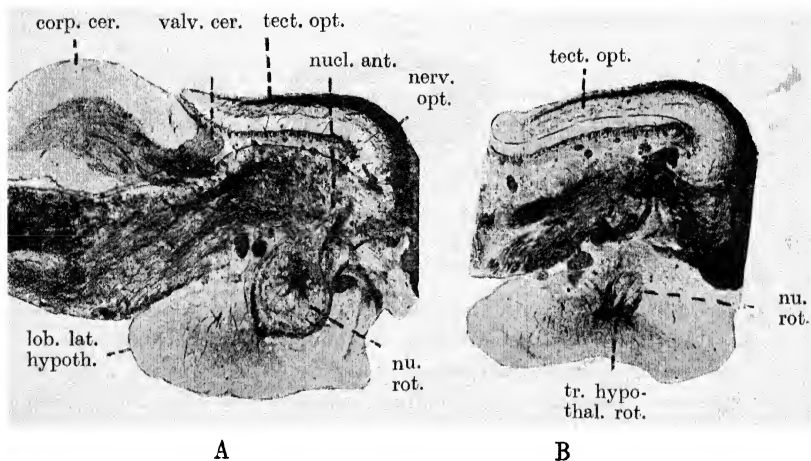
Fig. 60. Corpus glomerulosum of Syngnathus. The dorsal part (nucl. anterior in *A*) receives optic impulses, the ventral part (nucl. rotundus) impulses from the lobus lateralis hypothalami (see B).

Besides in many Teleosts the corpora geniculata are much larger

---

[1]) The epiphysis is small in most Teleostomes. In only a few representatives does a rudiment of neurosensory cells occur in it (STUDNICKA). Its fibers run in the posterior commissure and midbrain roof (N. HOLMGREN).

[2]) BRICKNER and CRAIGIE. Structural parallellism in the midbrain and tweenbrain of teleosts and Birds. Proc. Kon. Acad. v. Wetensch.. Amsterdam, Vol. XXX, 1927.

than in Plagiostomes, especially in Orthagoriscus (BURR [1])) and Pleuro-
nectidae (FRANZ). A typical feature of the tweenbrain is the *corpus
glomerulosum* of FRANZ (fig. 60 A and B), consisting dorsally of the *nucl.*
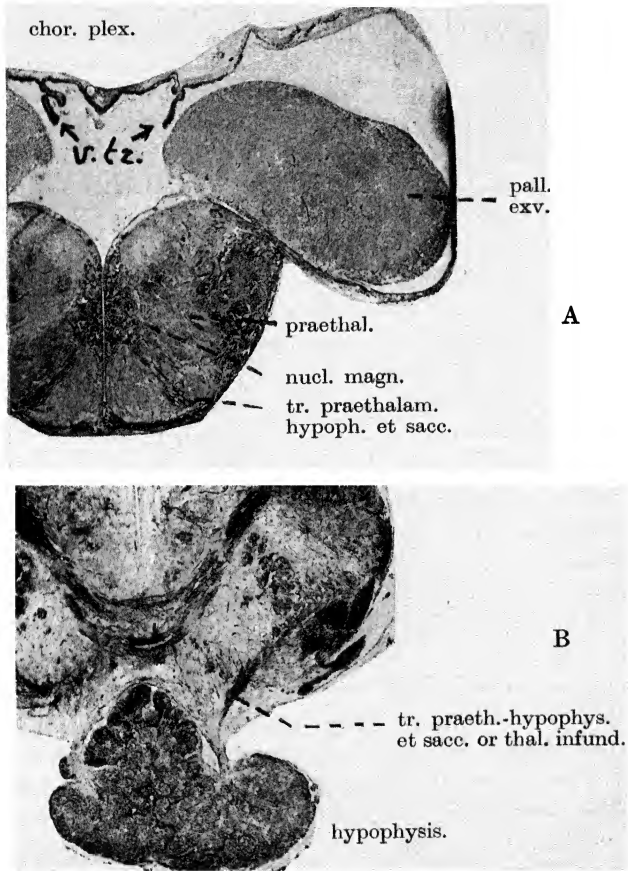
Fig. 61. Magnocellular praeoptic nucleus of Lota
lota and the tr. praethalamo-hypophyseos et sac-
cularis (or thalamo-infundibularis) arising from it.

anterior, ventrally of the *nucl. rotundus*. The whole complex originates

---

[1]) The central nervous system of Orthagoriscus mola. Journ. of Comp.
Neur. Vol. 45, 1928.

dorsally (FRANZ). Its dorsal *portion* (nucl. anterior) receives optic impulses (WALLENBERG, BRICKNER). that explain its position, but the larger ventral part, the *nucl. rotundus*, is connected with ventral forebrain fibers and with fibers from the posterior hypothalamic region (tr. hypothalamo-rotundus, fig. 60) and consequently migrates in a ventro-caudal direction [1] (CHARLTON: neurobiotaxis).

In the ventral part of the thalamus and hypothalamus, olfactory impulses are correlated with various impulses from the oblongata: equilibrium- (WALLENBERG), taste- (HERRICK) and touch-impulses from the head (spinal trigeminus nucleus, WALLENBERG). In addition the saccus vasculosus, best developed in deepsea fishes and least in surface swimmers (DAMMERMAN), provides it with perceptions of fluid pressure. The impulses of the saccus are partly elaborated caudally (GOLDSTEIN), partly coordinated with dorsal thalamic centres.

It is a remarkable fact that this organ lies so near the hypophysis, the secretion of which influences bloodpressure.

As in Plagiostomes, the large bloodvessels of the saccus are influenced by sympathetic fibers arising in the *magno-cellular praeoptic* nucleus (fig. 61 A) and in allied *ventral hypothalamic nuclei.*

The first nucleus, which is highly developed in Anguilla and Lota, is richly provided with bloodvessels, as is also the nucl. ventralis hypothalami near the hypophyseal stalk (CHARLTON). The latter is especially large in Belone (CHARLTON).

Other fibers of the same tract end in the hypophysis (fig. 61 B).

As in Plagiostomes, efferent fibers (tr. lobo-peduncularis) run from the hypothalamus to the oblongata, where they influence chiefly the branchial nuclei, while reticular oblongata cells may transmit their impulses to the cord. Thus, we see that the ventral thalamus and hypothalamus coordinate vitally important impulses and transmit them to regions, immediately connected with the maintenance of life.

The tweenbrain also has connections with the cerebellum. One, ascending(?) from the lateral hypothalamus, originates(?) behind the optic chiasm (tr. hypothalamo-cerebellaris). The descending brachium conjunctivum or tr. cerebello-diencephalicus ends partly in the ventral thalamus, but the majority of its crossed fibers run dorsally along the fasc. retroflexus (BRICKNER). Most of the latter fibers end

---

[1] The ventro-caudal migration of the nucl. rotundus explains also the peculiar course of a tectal commissure in these animals, the *commissura horizontalis*. For this and the other commissures I refer to my textbook.

in the region of the commissura posterior (*nucl. mesencephali dorsalis* of BRICKNER), where they are correlated with visual (geniculate ganglion and tectal) fibers. Descending tracts carry these correlated impulses to motor centers of the midbrain and bulb (BRICKNER).

The *midbrain* is essentially a correlation center for optic, static,
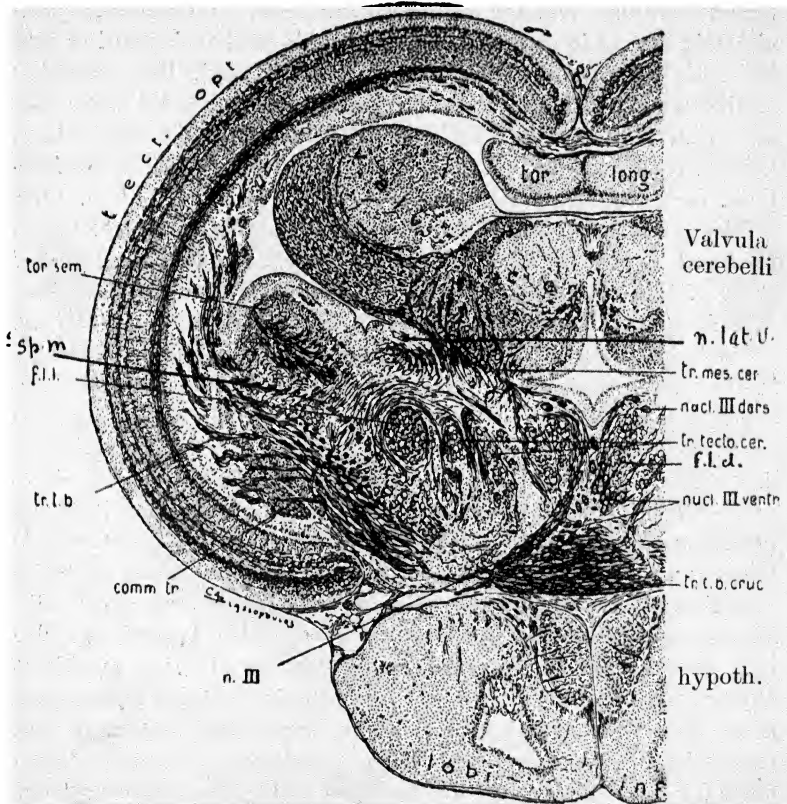
Fig. 62. Midbrain, valvula cerebelli and hypothalamus of Perca.
sp. m. = tr. spino mesencephalicus, f. l. l. = fasc. longitud. lateralis (lateral lemniscus); tr. t. b. = tr. tecto-bulbaris; comm. tr. = commissura transversa (between the tori semicirculares and tect); tr. t. b. cruc. = decussation of the tr. tecto-bulbaris; tr. mes. cer. = tr. mesencephalo-cerebellaris; f. l. d. = fasc. longitud. medialis or centralis.

protopathic cutaneous, and muscle sense impulses. It efferent tracts cause postural reflexes of the body and eyes.

Optic and muscle sense fibers end in its roof, static fibers underneath it, in the torus semicircularis (tor. sem., fig. 62).

A peculiar feature of the ganoid and teleostean optic tectum is the development of the *torus longitudinalis*, a ventricular outgrowth of the deep granular layer of the tectum (fig. 62). This torus is largest frontally, over the posterior commissure, and gradually diminishes in size as it passes caudally. Its cells send their neurites into the optic fiber layer of the tectum (SALA, KUDO). They probably receive cerebellar impulses by means of some toro-petal fibers that accompany the tecto-cerebellar tract [1]) and enter the torus above the posterior commissure. Also fibers originating behind the forebrain base are traced into the torus (KYOZO KUDO [2]), cf. p. 112).

This torus apparently is a neurobiotactic outgrowth of the tectum produced by toro-petal impulses. Its granular cells remind one of those of the cerebellum, also by their, unmyelinaled neurites, that spread, though not dichotomized, in the superficial tectum layer.

Static impulses end in the region beneath the midbrain ventricle, in the *torus semicircularis* (fig. 62), which is more differentiated from the lateral wall of the tectum than in Plagiostomes, and has become a centre per se. It receives projections from vestibular and lateral line centers in the oblongata by means of the *lateral lemniscus* or *fasc. longitudinalis lateralis* (f. l. l., fig. 62). In front of it, spinal projections (tr. sp. m.), carrying primitive cutaneous and muscle sense, run to the tegmentum and tectum. Underneath the posterior commissure lie the proprioceptive mesencephalic trigeminus cells. Mesencephalo-cerebellar fibers run from the nucleus lateralis valvulae into the valvula and corpus cerebelli (see fig. 62). From this it appears that the dorsal part of the midbrain (roof and tegmentum) is an important somatic center where optic, static cutaneous and muscle impulses are correlated. These correlations are partly transmitted to the cerebellum, by the *tecto-* and *mesencephalo-cerebellar tracts*, partly to motor centers of the midbrain and oblongata.

The direct and crossed tracts, running from the tectum and tegmentum of the midbrain, are the *tr. tecto-bulbaris* (t. t. b.), and *fasc. longitudinalis centralis* (F. l. d.). They convey impulses to the motor

---

[1]) This tract arises in the tectum and ends in the corpus cerebelli.

[2]) KYOZO KUDO. Ueber den Torus Longitudinalis der Knochenfische, and Eine frontale Verbindung des Torus longitudinalis. Anat. Anzeiger, Bnd. 56 und 57, 1923 and 1924.

eye nuclei of the midbrain and oblongata, and to the spinal cord,
largely by means of reticular cells. The tr. tecto-bulb. ventralis
ends partly in the inferior olive.

The *cerebellum* of Teleostomi is very different from that of Plagios-
tomes. In Ganoids only, Acipenser (JOHNSTON) and Polyodon (HOCKE
HOOGENBOOM), a clear distinction can be made between a corpus
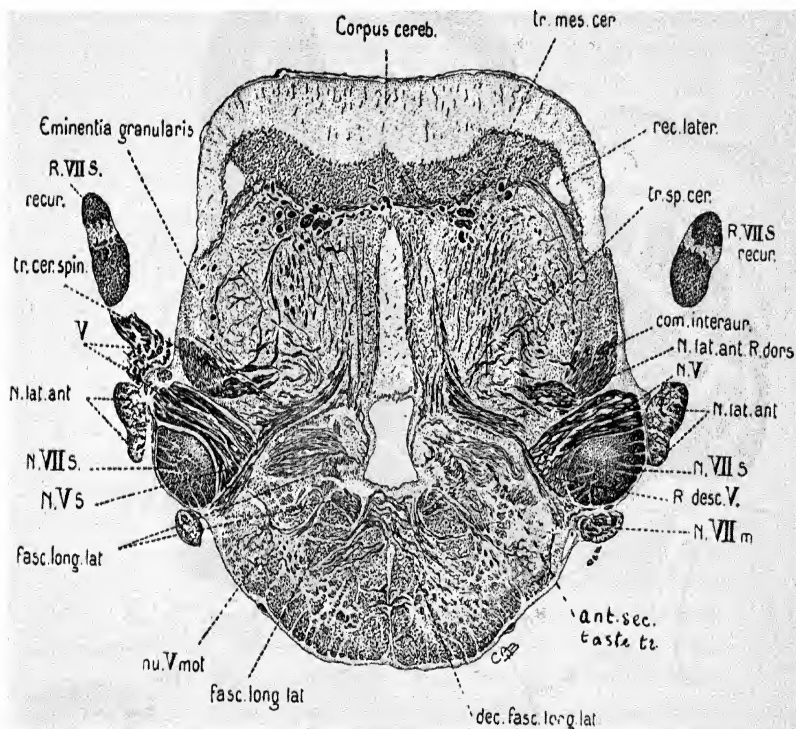
Fig. 63. Section of the oblongata and cerebellum of the Siluroid Arius. Note the
eminentia granularis cerebelli and the large sensory VIIth root.

and auriculi cerebelli, the latter being continuous with the static area
of the oblongata, which is covered with a *crista cerebellaris* (*pars bul-
baris cerebelli*, TILNEY), just as in Plagiostomes.

In most Teleosts auricles in the form of lateral recesses fail, but
the granular mass of the static area, covered caudally by the molecular
crista cerebellaris, comes frontally to the surface and forms the solid
eminentia granularis of FRANZ (fig. 63). This granular mass joins the

eminentia granularis of the other side by a subcerebellar granular layer (v. d. Horst) attached to the corpus, as also occurs in Plagiostomes with the granular masses of the auricles (*pars jugalis*, Tilney).

The eminentia granularis, like the auricles of Plagiostomes receives
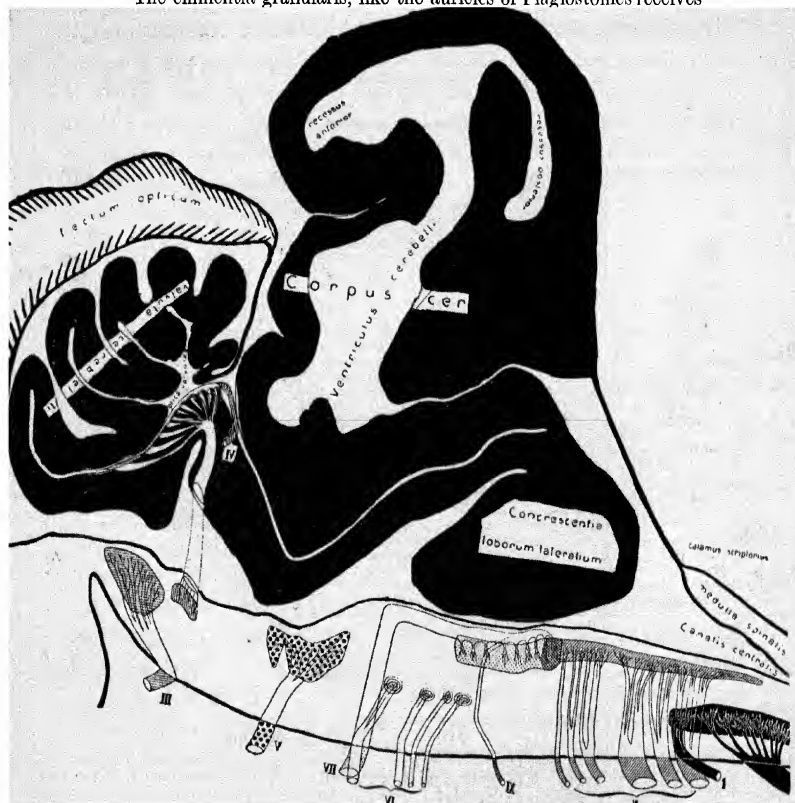
Fig. 64. The cerebellum of Megalops after v. d. Horst. Notice the strong developement of the valvula cerebelli from the basal cerebellar region and concrescentia lobor. N.N. later.

root fibers of the vestibular and lateral line nerves, and thus functionally resembles the latter (Addison).

A peculiar feature of the cerebellum is the *valvula*, (fig. 62 and 64), a frontal extension of the basi-auricular (*vestibulo-lateral*) region of the cerebellum protruding underneath the tectum. Its size

varies. It is very small in Amia and Lophius, very large in Thynnus and Megalops (fig. 64), but attains its greatest development in Mormyrus (STENDELL, FRANZ, BERKELBACH), where it even extends on the forebrain, protruding the roof of the midbrain as a thin lamella, which keeps its ordinary structure only at its lateral attachment to the tegmentum.

This frontal outgrowth of the basal cerebellar area is caused by impulses, which reach it from the tegmentum of the midbrain (tr. mesencephalo-cerebellaris, fig. 62) and is an interesting example of *neurobiotaxis*, showing the tendency of functionally related areas to establish connections and finally approach each other (cf. also p. 28 and 29).

The tegmentum where the mesencephalo-cerebellar tract arises (fig. 62) receives the *lateral lemniscus* from the static area. On the other hand, the basi-auricular region of the cerebellum receives static root fibers (especially lateralis fibers, ADDISON). This functional relationship of the basal cerebellar area and the tegmentum mesencephali is the neurobiotactic reason of the formation of the tr. mesencephalo-cerebellaris and of the outgrowth of the valvula.

That this topographical condition in Teleosts really depends upon the common relations of the parts involved with the static sense is shown also by the fact that the development of the valvula is most marked in such fishes, where the static sense, especially the N. N. laterales are most developed.

Concerning the way the cerebellar influence is elaborated, I have already mentioned that the fibers of the *brachium conjunctivum* run to the ventral thalamus and nucleus dorsalis mesencephali of BRICKNER, which correlates them with optic impulses. From here descending tracts run to the motor centers of the oblongata. Direct *cerebello-motor fibers* (KAPPERS) enter the fasc. longit. medialis, some ascending to the oculomotorius nucleus, but most of them descending to bulbar and spinal somato-motor centers, accompanied by a similar system from the static area (*octavo-motor fibers*).

Also the *oblongata* shows considerable differences from the conditions found in sharks. These differences concern the sensory as well as the motor system. In the *sensory roots*, with the exception of the trigeminus, the general visceral and the taste fibers predominate. Only the *vagus* constantly keeps a general cutaneous branch in all vertebrates, joining the descending V (fig. 66). The *facial nerve* contains

general cutaneous fibers in *Amia*, *Lepidosteus* (NORRIS) and, a great many, in *Albula* (V. D. HORST). In all other Teleosts, hitherto examined, the facial and glossopharyngeal nerves contain only visceral fibers. These viscero-sensory components are much increased in most Teleosts, largely as a consequence of the increase of *taste fibers*.

The greatest increase and spread of *taste buds* occurs in Cyprinoids and Siluroids, where they are found on the whole head and body, being innervated by branches of the facial nerve (HERRICK). This increase of the taste fibers in the facial nerve is responsible for the considerable size of the sensory VII root (cf. fig. 63). The number of taste fibers in the glossopharyngeus and vagus (cf. fig. 66), though not extending over the head or body, has also increased in these animals.
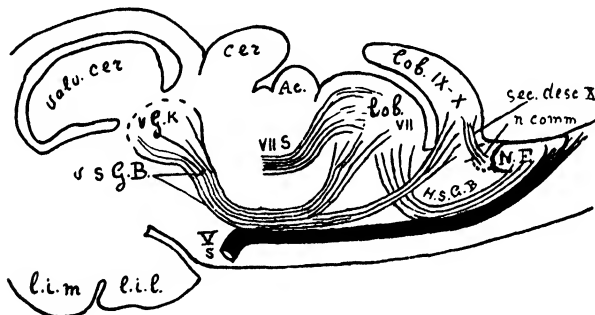
Fig. 65. Secundary taste tracts in a Cyprinoid (HERRICK).

Thus we find in nearly all Teleosts, but especially in Cyprinoids and Siluroids, an enlargement of the sensory VII, IX and X nuclei which may surpass the size of the cerebellum. From these nuclei a descending tract (H. S. G. B.) runs to the cervical region (N. F.). A larger ascending bundle (V. S. G. B.) ends in the frontal gustatory nucleus (V. G. K.). From this nucleus tertiary taste fibers run to the hypothalamus (HERRICK) and to the tectum (BRICKNER), thus proving, that taste impressions have widely spreading correlations in these animals.

The ascending taste tract has a remarkable influence on the position of the motor nuclei of the facialis and trigeminus, the topography of which in most Teleosts is very different from that in Plagiostomes, being determined by this large tract that runs

ventrally along the descending V root (fig. 65, 66), and not, as in Plagiostomes, and in primitive Teleosts (fig. 64), by short local neurones.

Fig. 67 presents the arrangement of the cranial motor nuclei in Petromyzon, Scyllium and Tinca. From this it appears that, whereas

fibr. extern. (capsulares).

Nu. mot. X

sec. gust. tr.

V desc.

fibr. centrales

rad X mot
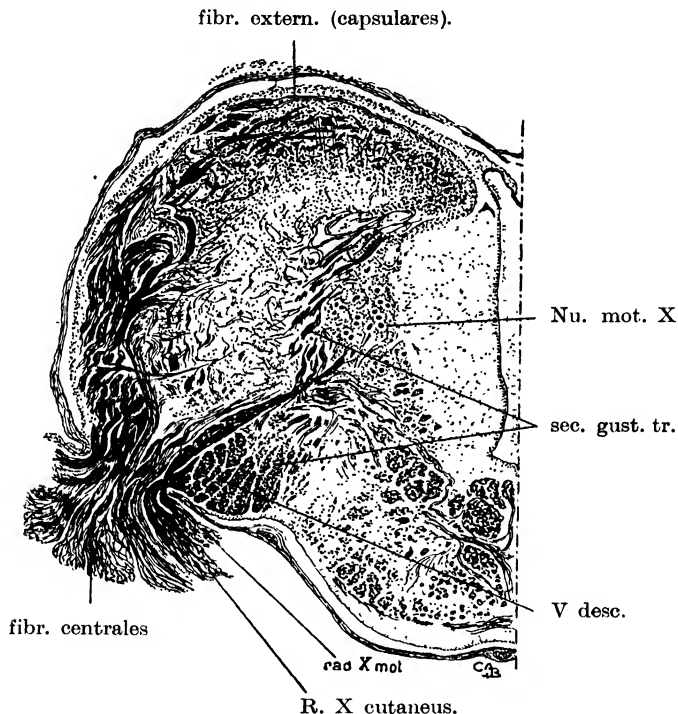
R. X cutaneus.

Fig. 66. Vagal lobe of Tinca tinca. Note the general cutaneous fibers of the vagus (R. X cutaneus) joining the descending trigeminus (V desc.), while its viscero-sensory fibers enter the dorsal lobe. Of the latter the capsular fibers are chiefly taste fibers, the central ones being general viscero-sensory. A strong secondary gustatory tract runs medially to the descending V. The motor X nucleus lies medially to the sensory X nucleus.

in sharks the motor VII nucleus forms the frontal continuation of the IX and X, all three lying dorsally near the sensory centers of the gills, in Tinca only the motor IX and X nucleus have kept an entirely dorsal position (fig. 66). Most of the VII cells have
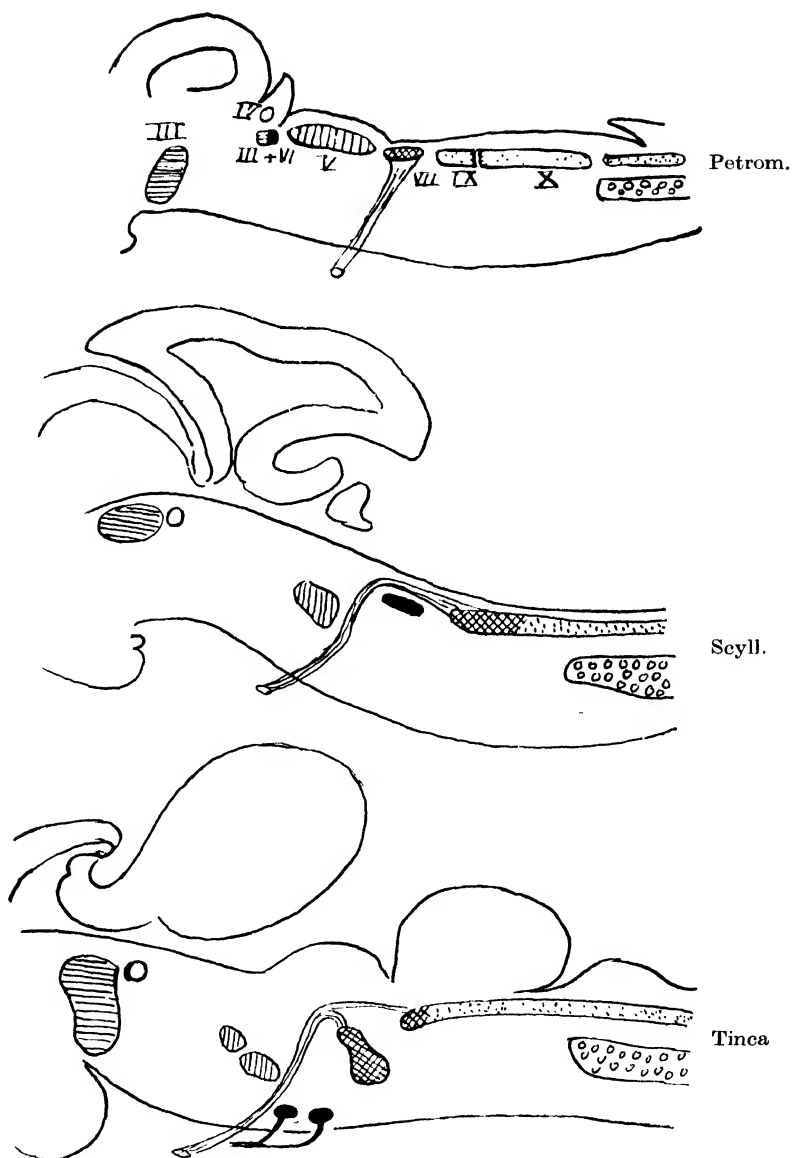
Fig. 67. Arrangement of the cranial motor nuclei in Petromyzon, Scyllium and Tinca. Horizontally striped = III nucleus; open = IV nucl.; perpendicularly striped = V nucl.; black = VI nucl.; crossed = VII nucl.; dotted IX and X nuclei; open dots spino-occipital nucleus (XII).

shifted frontally and ventrally along the frontal gustatory tract
which also has determined the more ventral |position of the hind
part of the motor trigeminus nucleus (fig. 67).

The eye muscle nuclei show equally conspicuous changes.
The III nucleus, lying dorsally in sharks, near the fasc. longitu-
dinalis medialis, partly has a dorso-lateral, partly a medio-ventral
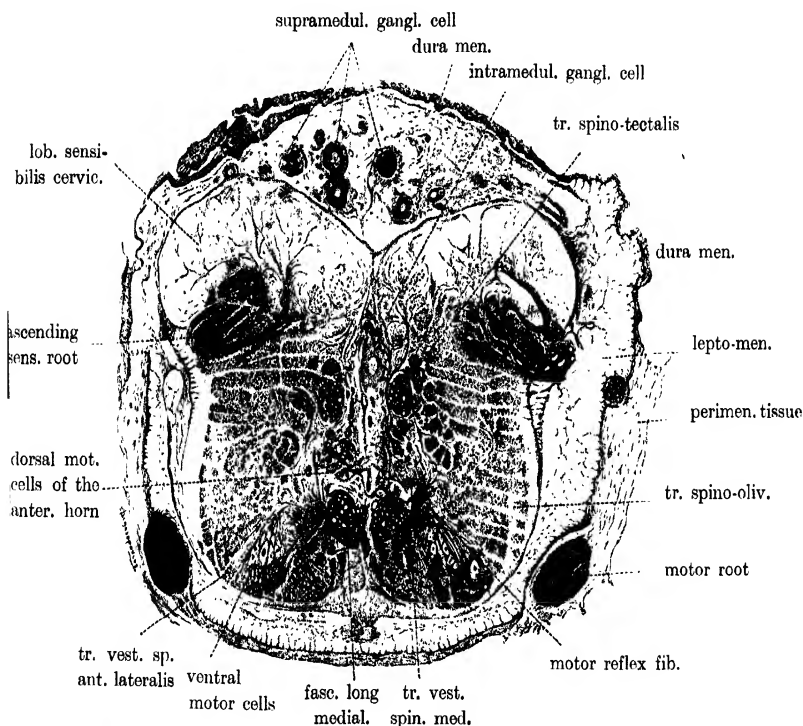
Fig. 68. Upper cervical cord of Lophius piscatorius, in the meninges (cf. p. 192).

position in Teleosts. Whereas the IV nucleus has the same posi-
tion in Teleosts as in sharks, underneath the ventricle near the
III nucleus, the *abducens* nucleus, contrary to its topography in
Plagiostomes, lies ventrally in Teleosts, a consequence of the pre-
vailing influence of the large ventral tecto-bulbar reflex tracts.

So we see that the different organization of the reflex pattern causes
considerable differences in the location of the motor root centers.

The *spinal cord* of Teleosts resembles that of sharks. A marked difference is seen only in certain species such as Orthagoriscus and Lophius, where a considerable reduction of its caudal part has occurred, in consequence of the atrophy in the tail region. In these species, the vertebral canal is almost entirely filled with root fibers (cauda equina), retaining in their midst a very long filum terminale. In most Teleosts, however, the cord extends into the tail region and here generally shows a ventral thickening consisting of glandular cells and glious tissue. This is the so called "hypophysis spinalis" (VERNE, FAVARO), which in the lamprey and in sharks is only indicated by the glandular poly-nuclear cells of DAHLGREN and SPEIDELL.

In some Teleosts in which the anterior fin rays are developed into organs of exploration (Lophius, Trigla and Prionotus; HERRICK), the cervical cord shows an enlargement of the sensory horns (fig. 68) which, however, has nothing in common with the nuclei of GOLL and BURDACH (fig. 86) in the cervical region of the posterior funiculi in mammals. The cervical sensory lobes in fishes are merely the result of a local hypertrophy of the first cervical roots, whereas the nuclei of the posterior funiculi in mammals receive ascending rootfibers from all segments of the spinal cord.

As we shall see (p. 156) the large posterior funiculi of mammals subserve a higher, stereognostic sense while the skin of fishes (like the cornea and gingiva in man) is probably only susceptible to primitive or *vital* sensations (protopathic, HEAD, or dyscritic sensi-bility, PARSONS) pain, very high and low temperatures, and a poorly localized feeling of touch, as are perceived by simple nerve endings in the skin. Even the muscle sense of fishes is perceived largely by intermuscular, capsuled endings, true muscle spindles and musculo-tendinous terminations occurring chiefly in higher vertebrates.

Since the primitive or *vital* sensations in mammals mostly end in the substantia gelatinosa of the posterior horns (RANSON), it is not strange that this substance is more developed in fishes than the rest of the posterior horn (KEENAN).

In Albula VAN DER HORST even found a very considerable gelatinous substance, lamellated and folded, as is also observed in the sacral region in Ungulates (BIACH).

In connection herewith it is interesting that Albula also has a

hypertrophy of primitive skin sensibility in the headregion as appears from its large cutaneous facial root (p. 120).

But also in Mugil chelo, Amia and several other Teleosts, KEENAN [1]) found a considerable development of the substantia of Rolando in the cord.

In many Teleosts large *intra- and supramedullary sensory root cells* are found (fig. 68), inside and on the dorsal surface of the cord, especially in the cervical region. These cells are homologous to the transient intra-spinal cells in the larvae of sharks (ROHON and BEARD), Amphibia (HERRICK and COGHILL) and Reptiles (VAN GEHUCHTEN), but in several Teleosts they remain during life. They probably serve both skin and muscle sensibility as they may do in worms (p. 31).

The sensory horns of the cord are projected on the midbrain by EDINGER's crossed *spino-mesencephalic tract* (collaterals of which run to some motor oblongate nuclei), and on the cerebellum by the uncrossed *tr. spino-cerebellaris*. Other ascending fibres run to the *inferior olive*, which is small and rather diffuse in these animals (KOOY). From here their impulses are transmitted contro-laterally to the cerebellum.

The descending tracts to the cord are practically the same as in sharks (p. 107). MAUTHNER's fiber only, running from the vestibular region to the tail region, should be mentioned (cf. BARTELMEZ).

In Teleosts it generally arises from one large cell, as it does in Amphibia (DETWILER, BECCARI).

In Ceratodus (a Dipnoan) this giant fiber arises from the union of several axones (V. D. HORST). as do the giant nerve fibers in most Annelids (cf. p. 36).

Some Teleosts (Malapterurus, Gymnotus, Mormyrus) have electric organs. Those of Gymnotus and Mormyrus are innervated by ventral spinal roots, those of Malapterurus by dorsal motor branches [2]), the organs of the former being derived from somatic musculature, the others from unstriped musculature of the skin.

---

[1]) KEENAN. The phylogenetic development of the substantia gelatinosa Rolandi. Proc. of the Kon. Akad. v. Wetensch. Amsterdam, 1928.

[2]) The electric organ of Torpedo is also innervated by the motor branches of visceral (branchial) nerves (the VII, IX and X).

FURTHUR DEVELOPMENT OF THE FOREBRAIN IN AMPHIBIA, REPTILES, BIRDS AND MAMMALS.
The striatum.

I shall not deal with all the regions of the central nervous system in Amphibia. In many respects, especially in tailed Amphibia, their structure recalls that of the Plagiostomes.

In adult Anura the spinal cord is reduced, the part corresponding with the lost tail being atrophied to a thin filum terminale, which in the frog begins between the sixth and seventh vertebra, in Pipa already at the third (TENSEN [1]).

The most important difference in the oblongata is the absence of lateral line nerves and their centers in adult terrestrial Amphibia [2]). In consequence of this also the crista cerebellaris, which in fishes and most tailed Amphibia covers the lobi liniae lateralis, is lacking here.

Also the cerebellum itself is reduced. It consists of a single plate, representing the corpus cerebelli, and paired auriculi, the former, as in fishes connected with hypothalamo-, tecto- and spino-cerebellar, the latter with primary and secondary vestibular fibers (HERRICK, LARSELL [3])).

The midbrain resembles that of Plagiostomes, only in Anura the tori semicirculares are more developed but the tweenbrain is reduced in its hypothalamic part (where a saccus vasculosus is also lacking), while the dorsal thalamic region (including the lateral geniculate nucleus) is enlarged, a symptom of higher development.

The *forebrain* of these animals, however, is more interesting to us, as it forms the prototype of the forebrain of higher vertebrates.

As in Plagiostomes, it is built after the inverted type (cf. fig. 58).

On a transverse section, each hemisphere may be divided into four parts (fig. 69). The two dorsal parts are the palaeo-pallial and the archipallial areas. The ventral parts are the striatal and septal regions.

---

[1]) TENSEN. Einige Bemerkungen über das Nervensystem von Pipa pipa. Acta Zoologica, Bnd. 8, 1927, p. 151.

[2]) In the waterliving Amphibia and larvae of terrestrial Amphibia they occur.

[3]) LARSELL. The development of the cerebellum in the frog (Hyla regilla) in relation to the vestibular and lateral-line system. Journ. of Comp. Neur., Vol. 39, 1925.

The lateral part of the pallium, the *palaeo-cortex*, receives chiefly secondary olfactory fibers from the mitral cells (olfactory tracts).

It is the primitive homologue of the cortex praepiriformis of mammals.

The lower part of the lateral mantle region shows a ventricular protrusion, more or less analogous to the *epistriatum* of fishes, but smaller, and receiving also olfactory tract fibers (HERRICK [1])).
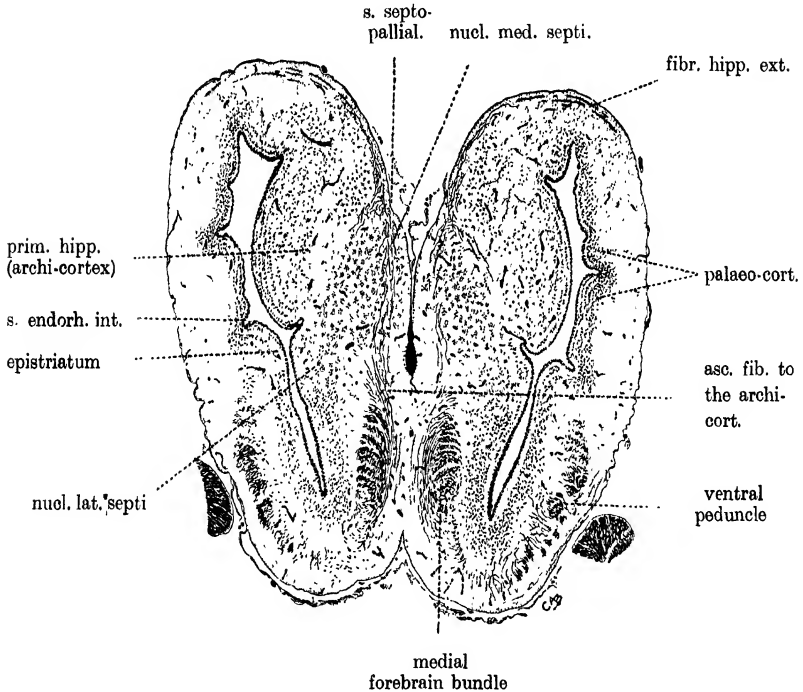
Fig. 69. Forebrain of Rana catesbyana, in front of the foramen MONROI.

The epistriatum begins some distance in front of the foramen MONROI (fig. 69). Extending backward in the lateral wall, its protrusion decreases gradually until it disappears just before the hindpole of the hemisphere.

---

[1]) HERRICK found that the fibers of the accessory olfactory bulb — a special part of the bulbar formation in frogs — terminate here. I can only confirm this.

The medio-dorsal portion of the mantle, *archicortex* or *primor-dium hippocampi*, receives, next to secondary, higher (tertiary) olfactory fibers and probably visceral projection fibers (HERRICK) from the hypothalamus.

Of the two ventral areas, the *septum* (fig. 69) is important on account of the fact that it is an intermediate station for ascending

For. Monroi.

archicortex or
primord. hipp.

palaeo-cort.

comm. pallii.

epistriatum.

p. fimbr. septi

palaeostriatu

comm. ant.

tr. strio-tha
et hypothal
or ventr.
pedunc.

nu. praeopt.

recessus praeopticus.
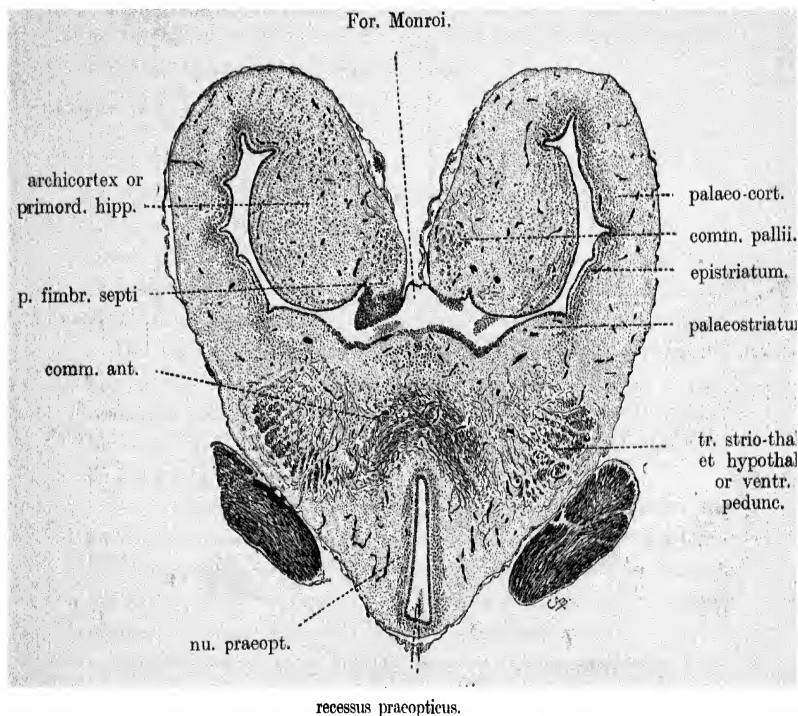
Fig. 70. Section through the forebrain of Rana catesbyana, on the level of the foramen of Monro.

(nucl. septi lateralis) and descending fibers (nucl. septi medialis) of the hippocampus (HERRICK, RÖTHIG).

The amphibian *striatum* (fig. 70) is very simple and only repre-sents the oldest part of the striatal complex of higher vertebrates: the *palaeo-striatum*. It arises on the level of the praeoptic recess (fig. 70), the end point of the sulcus limitans, and lies medially to the backward continuation of the epistriatum. It is not directly

(perhaps indirectly) connected with olfactory impulses, but receives some fibers from the ventral thalamus and hypo-thalamus, probably visceral connections, and sends large efferent neurones to these regions, the strio-hypothalamic tract or ventral peduncle (fig. 69, 70).

In this peduncle occur cells (nucl. peduncularis) which reinforce the tract, and so are functionally related to the cells of the palaeostriatum (similarly as the substantia nigra in mammals).

In *reptiles* the forebrain is much more differentiated. I shall de-
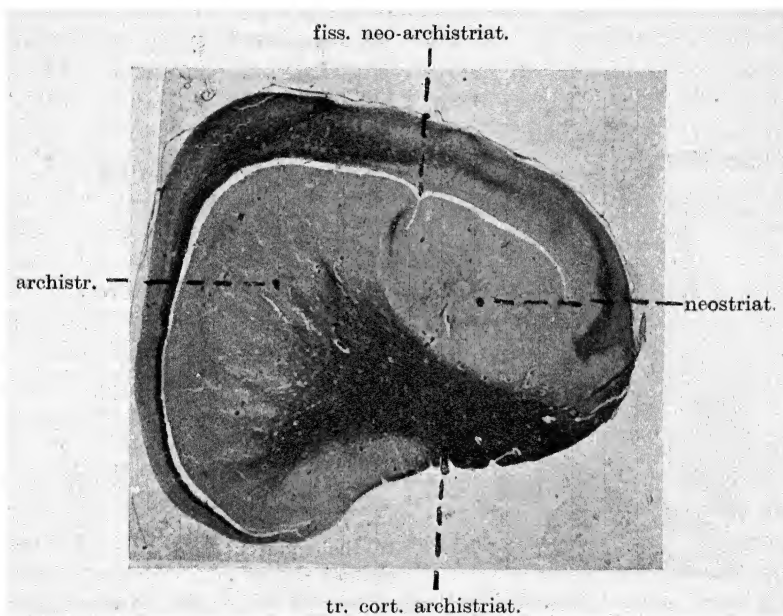
Fig. 71. Sagittal section of the forebrain of Varanus salvator, lateral to fig. 72.

scribe its relations in Varanus (for the Alligator, see CROSBY).

Both the lateral epistriatum and the medial palaeostriatum are found again in Reptilia, but with new differentiations added.

The *epistriatum* is represented in Reptiles by a lateral group of cells, a little behind the insertion of the olfactory stalk, and generally referred to as the *lateral olfactory nucleus* (CROSBY); it receives, as it does in frogs, olfactory fibers, though also here most of these fibers terminate in the lateral or palaeo-cortex.

This structure is, however, entirely surpassed in Reptiles by the addition of a *secondary* epistriatum or *archistriatum*, which developes from the lateral hemispherical wall behind this nucleus and does *not* receive olfactory tract fibers, but fibers arising in the (olfactory) palaeo-cortex, the tr. cortico-epistriaticus of EDINGER, better termed *Tr. cortico-archistriaticus* (fig. 71).

The archistriatum forms the most caudal part of the intraventricular complex, and reaches to the hindpole of the mantle, just as does its mammalian homologue, the *amygdala*.

The archistriata of both sides are connected by a *commissura*

fold of the mantle   fiss. archi-neostr.

fiss. palaeo-neo striatica

primord. neo-pallii

tr. cortico-archistr.

tr. thalamo-front. et fronto-hypoth.

tr. thal. neostr.
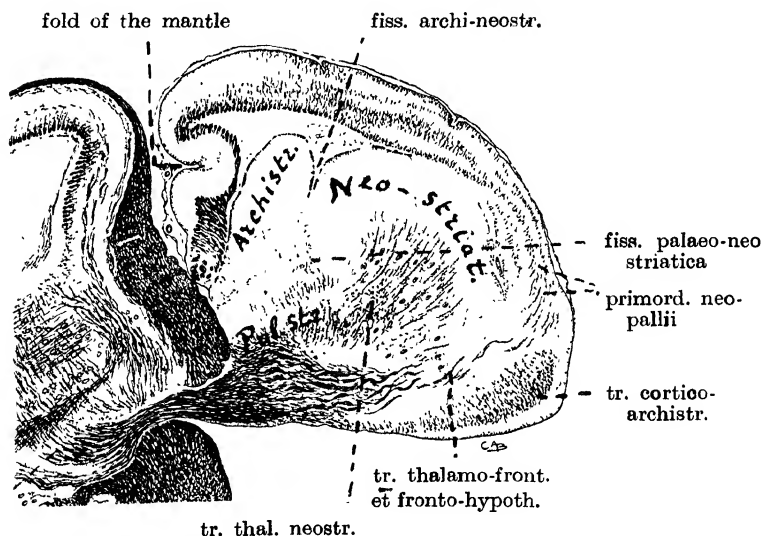
Fig. 72. Sagittal section of the forebrain of Varanus salvator, medially to fig. 71, showing the three parts of the striatal complex and the thalamo-neostriatal tract.

archistriatica, and from them an efferent tract (WILLIAM HERMAN [1]) runs to the hypothalamus and mesencephalon.

Medially and ventrally to the archistriatum lies the *palaeostriatum* (fig. 72, pal. str.), consisting chiefly of large cells.

As in frogs, it is best developed on the level of the foramen MONROI, covered, however, in reptiles dorsally and laterally by the archi-

---

[1] The relations of the corpus striatum etc. Brain, vol. 48, 1925.

striatum and in front by the third and most important component of the striatal complex of these animals: the *neostriatum* (fig. 72).

The *neostriatum* is continuous with the palaeostriatum (fig. 72), from which it is delimited medially by a shallow fissure (*fiss. palaeo-neostriatica*).

In Varanus it is separated from the archistriatum by a very deep fissure (*fiss. archi-neostriatica*).

The neostriatum developes partly from the basal wall of the forebrain and partly from the mantle, with which it is frontally continuous (W. HERMAN, see fig. 72).

The connections and functions of the three parts of this complex differ. Those of the archistriatum have been already mentioned; they are chiefly olfactory, and efferent hypothalamic (W. HERMAN).

The palaeostriatum, as in Amphibia, is a prevailing *efferent center* for the ventral thalamus and midbrain, where its neurites terminate on peduncular cells, from which it may receive also some ascending fibers, as in fishes and Amphibia.

The neostriatum in reptiles is mainly *receptory*, receiving ascending neurones from the *inner segment of the dorsal thalamus*, which has become much larger in reptiles, where it is differentiated in an *anterior, medial* and a small *ventral nucleus*, forming together the *neothalamus* of these animals.

The character of the stimuli thus received is not exactly known: probably they are a correlation of impulses from the trigeminus and olfactory impulses (*oral sense*, KAPPERS), since the medial nucleus (in mammals) is connected with secondary trigeminus fibers, whereas the anterior thalamic nucleus is connected with the mammillary area of the hypothalamus, where fornix fibers from the hippocampus end. From this it is probable that the neostriatum of reptiles is largely concerned with the head and probably in some way has to do with feeding instincts.

In *birds* the same striatal components are found as in Reptiles.

In addition, however, a new intraventricular outgrowth of the dorso-lateral and frontal pallium occurs, the *hyperstriatum* of EDINGER (d, fig. 64) which only fails in the humming bird (CRAIGIE [1])) and

---

[1]) Observations on the brain of the humming bird. Journ. of Comp. Neur., Vol. 45, 1928.

which varies in size in the other orders, being largest in the parrots (HUBER and CROSBY).

The *palaeo-striatum*, immediately in front of the foramen Monroi, attains a much larger size than in Reptiles and is known as the *meso-striatum* (b, fig. 73). In its center, the primitive palaeostriatum is represented by the large efferent neurones, that form the tr. *strio-mesencephalicus*[1]) *et hypothal.* to which, however, a great number of smaller cells are added (palaeostriatum augmentatum), indicating a secondary increase, which may be due to cerebellar connections (*tr. cerebello-striatalis*: SCHROEDER, CRAIGIE).

In fig. 73 behind this, a small part of the *archistriatum* or
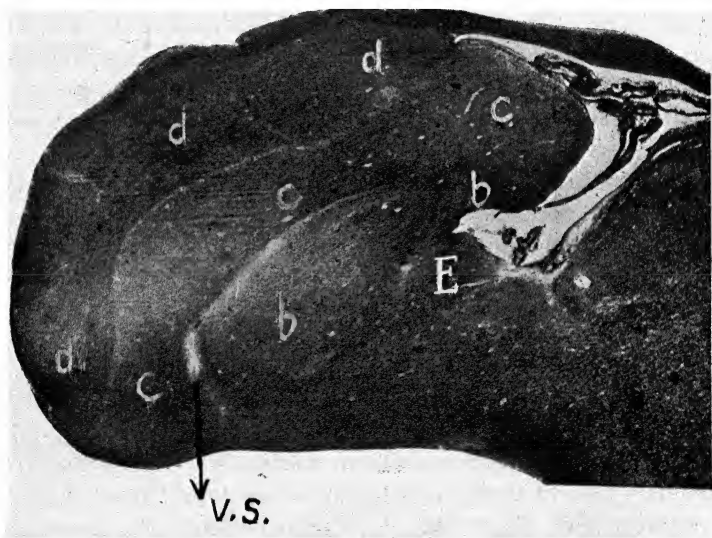
Fig. 73. Sagittal section of the forebrain of a chick embryo of 11 days.
(V.S. = limiting artery between b and c.)

amygdala (E) is visible. On more lateral sections this appears to be fairly large, which seems astonishing, since birds (with the exception of the Kiwi: HUNTER) are microsmatic.

Its size, in birds, is a decisive argument to show that the existence of the archistriatum can not depend upon olfaction alone. This is confirmed by the fact that the region of origin of the cortico-archi-

[1]) To the spiriform and reticular nuclei of the midbrain (WALLENBERG).

striatic tract in these animals, the palaeo-cortex, also receives a secondary tract from the homo- and contralateral *frontal trigeminus nucleus* (WALLENBERG, cf. p. 164). This points to an intimate correlation between olfaction and other impulses from the head (proprioceptive and exteroceptive)[1], an *oral sense* association (KAPPERS) neurobiotactically explained by the frequent correlation between smell and head sensibility.

Here, also, the archistriata of both sides are commissurally connected and send an efferent tract to the mesencephalon (tr. occipito- or better archistriato-mesencephalicus of WALLENBERG and A. HERMANN[2])).

The *neo-striatum* (C) in all birds, except the humming bird (CRAIGIE), is much larger than in reptiles, but developes in the same way and arises partly in front of the palaeostriatum from the basis of the forebrain (fig. 73), partly from the lateral mantle.

Its greater size apparently depends upon the further differentiation of the neothalamic nuclei, of which the nucleus medialis (nucl. rotundus in birds, INGVAR) has greatly increased, by taking up fibers from the midbrain (tr. tecto-thalamicus), thus adding also optic and static[3] impressions to the striatum, which do not yet occur in it in Reptiles.

So the avian neostriatum establishes many correlations, receiving sensory, static and optic impressions of vital importance.

The fibers from the anterior and dorsal thalamic nucleus end in the medial part of the neostriatum, fibers from the nucl. rotundus end in the lateral neostriatum (WALLENBERG).

The neostriatum in birds has also several *efferent connections* (WALLENBERG, SCHROEDER) with the nucl. rotundus.

These fibers partly arise from the lateral part of the neostriatum, near the so called *ectostriatum*.

The most dorsal part of the striatal complex of birds, the *hyperstriatum*, originates entirely from the fronto-dorsal and lateral pallium and therefore might be better called *hypopallium* (ELL.SMITH)[4].

---

[1]) It is probable that the tr. quinto-frontalis of WALLENBERG carries also proprioceptive impulses, since the sensory V nucleus, from which it arises, sends also fibers to the cerebellum (BIONDI, CRAIGIE).

[2]) Beiträge zur Anatomie des Vogelgehirns. Anat. Anz., Bnd. 40, 1925.

[3]) The tectum of birds — as in fishes — receives fibers from the lateral (VIII) lemniscus.

[4]) ELL. SMITH used this name for the whole striatum, except the palaeostriatum; it seems, however, especially adapted to the hyperstriatum.

Its ventricular growth may be favored (ELL. SMITH, DART) by neurobiotactic influences of ascending tracts from the thalamus that end in it and by its fiber relations with the neostriatum, with which, in the adult, it entirely coalescesces. SCHROEDER found several fibers connecting these parts.

The afferent connections of the hyperstriatum are practically the same as those of the neostriatum. Whether, however, efferent fibers arise in it, is doubtful.

The outgrowth of the hyperstriatum, reduces the ventricle to a narrow split, especially in parrots, less so in other birds (CROSBY). It seems to replace a surface extension of the pallium similarly as the epistriatum in Teleosts replaces a surface extension of the (palaeo-) pallium (cf. p. 109). Like the epistriatum in Teleosts, its massive form may be influenced by mechanical factors preventing the mantle from growing out in a normal manner (by surface extension), the brain of birds being very narrowly enclosed in the skull.

The physiology of the avian striatum and hyperstriatum has been experimentally examined by ROGERS, who did not find strictly localized functions in it, but observed that the emotional actions of the animals, as courting, feeding and fighting movements, gradually deteriorate, when a larger part of it is removed. In addition, ROGERS found a center of blood pressure to be localized here which, after all, is not strange, as the striatum developes just in front of the frontal end of the sulc. limitans, along which the sympathetic centers lie.

Also in human striatal degenerations, the emotional behavior is more impaired than the intellectual actions. I remember a patient with striatal lesions, who could perform higher, apparently cortical movements fairly well, but who was very much impaired as soon as emotions came in.

Also this fact is in favor of the conception that the striatum includes sympathetic functions (cf. p. 138), as emotions are closely linked up with sympathetic innervations.

The excessive development of intraventricular masses in birds is in strong contrast with the poor development of the cortex.

A differentiation of the cortex into layers of cells does not even occur, except in the palaeo — or praepiriform cortex (HUNTER, ROSE). The cellular arrangement in the remaining cortex is quite undifferentiated. The dorsomedial pallium, however, plays a part of importance, as a motor centre, giving origin to the tr. cortico-mesencephalicus septi, that terminates in the tectum and near the oculomotor nucleus (WALLENBERG, SCHROEDER).

The *striatum* in mammals, is built on the same principle as that of reptiles.

Apart from the archistriatum or *amygdala*, only a *palaeo-striatum* and a *neo-striatum* may be distinguished. The palaeo-striatum arises first. It originates directly in front of the praeoptic recess, about the foramen Monroi. The neostriatum originates later (E. DE VRIES), partly from the basis, partly from the mantle (crus epirrhinicum of His). As in Reptiles and birds it extends more frontally than the palaeo-striatum (fig. 74, at the right).

Separated in embryos by a deep furrow, the *fiss. palaeo-neo-striatica*, (see fig. 74), the relation between these two parts soon changes, the neo-striatum increasing much more in size and soon

Fig. 74. Transverse section of the striatal region of the forebrain in a human embryo of 27 m.m. The right side is slightly more frontal than the left where the primo:dium of both the neo- and palaeo-striatum are seen, separated by a deep palaeo-neostriatal furrow.

covering the palaeo-striatum entirely, so that nothing, or only a vestige of the separating furrow is left on the medial ventricular side of the striatal complex (see fig. 75).

In adult mammals the neostriatum is represented by the *caudate nucleus* and *putamen*, and the palaeostriatum by the *globus pallidus*, which in mammals is also continuous with cells of the ventral thalamus and midbrain base (corpus subthalamicum and substantia nigra), as it is continuous with peduncular cells in lower verte brates.

The division made in the mammalian neostriatum by the internal capsule has no intrinsic significance. Moreover, the location and extent of this capsule varies and frontally it fails in all mammals.

Compared with birds the neostriatum of mammals has increased, and its form has changed being caudally extended (fig. 76) along the thalamus to the cornu inferius of the ventricle, where it joins the archistriatum or amygdala that remains attached to the posterior part of the piriform lobe, as it does in reptiles and in birds.

neostr. (nu. caud.)

fiss. palaeo-neo str.

septum

taenia semic.

ant. comm.

(putamen) neostr.

glob. pallid. (palaeo-striat.)

subcomm. part
of the palaeo-str.
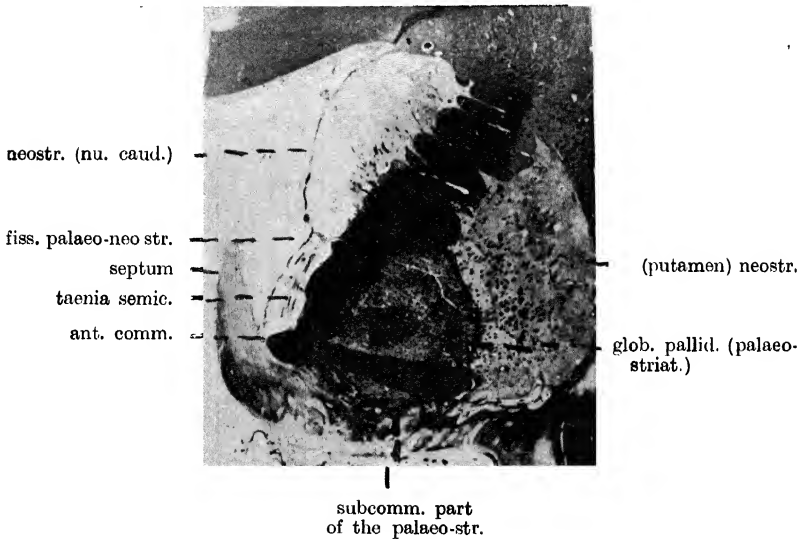
Fig. 75. Transverse section of the corpus striatum of an adult man on
the level of the anterior commissure.

This extension of the neostriatum is a consequence of the caudal elongation of the hemisphere.

Although the striatum in mammals has increased, this increase by no means keeps pace with that of the neopallium, with which it is connected in mammals (COENEN, WALLENBERG, INUI, WINKLER), and man (MINKOWSKI), with the frontal and central cortex chiefly.

The character of the striatum is principally the same as in reptiles, the neo-striatum being chiefly receptive and correlative, the palaeostriatum largely efferent.
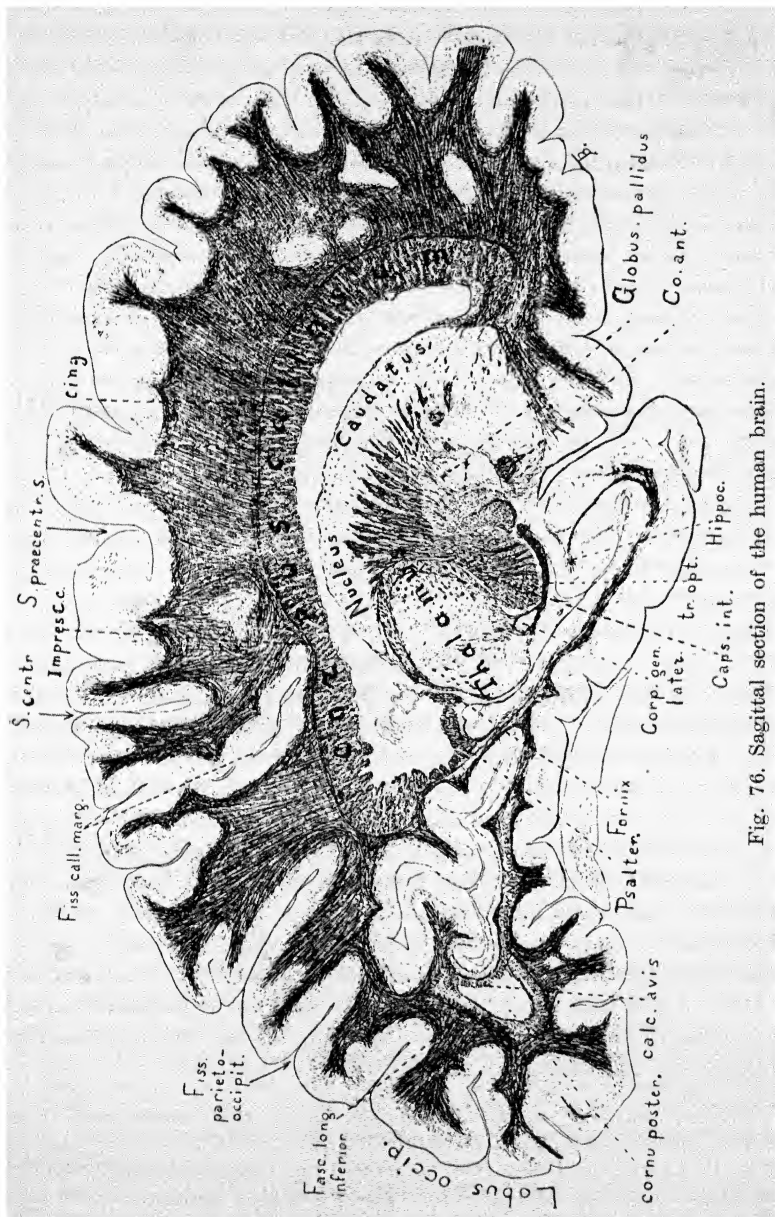
Fig. 76. Sagittal section of the human brain.

So in the striatum a similar relation occurs as in the cortex (p. 143 and 144), where the upper layers, which are also phylogenetically younger, are receptive and correlative, the deeper layer being chiefly efferent in character.

The neostriatum receives fibers from the anterior and medial thalamic nuclei (KAPPERS) and from part of the ventral nucleus (VOGT, INGVAR). Among these are probably sympathetic impulses from the (juxta) ventricular thalamic region and *proprioceptive* impulses of the head and body. The palaeostriatum receives fibers from the substantia nigra (= peduncular nucleus of amphibia, reptiles and birds) and it sends neurites to the substantia nigra and corpus subthalamicum. In addition to these it sends fibers to subcerebellar centers, the nucl. ruber and inferior olive (WALLENBERG, WINKLER).

As regards the *function of the corpus striatum*, we know that it has to do with motility, since it is degenerated in such spastic conditions as in PARKINSON'S and WILSON'S disease, and sometimes in chorea (JELGERSMA, RAMSAY HUNT, VOGT, LEWY).

It is interesting to note that in the striatal disturbances occurring in consequence of encephalitis lethargica those activities which may be considered as vital and emotional activities are particularly impaired (cf. p. 134).

The higher movements, which depend to a greater extent upon cortical innervation, are in such cases much less disturbed.

Tonus is also influenced by the striatum (MILLS a. o.). This may be explained by its relation with the proprioceptive mechanism, or by the sympathetic innervation of voluntary muscles, discovered by BOEKE and confirmed by many others (cf. p. 86). Degenerations of the striatum, especially of the neostriatum, may be accompanied by definite sympathetic disturbances, e.g. of the bladder [1]), (CHYHLARZ, MARBURG, VAN DER SCHEER, STUURMAN, BROUWER), perspiration and intestinal functions (see especially LEWY's work on the vegetative nervous system [2])).

The influence of the striatum on the sympathetic is not strange in view of the fact that the striatum developes just in front of the ending of the sulcus limitans (fig. 45), along which the central sympathetic is located.

---

[1]) Another center of the bladder lies just behind the posterior end of the midbrain, near the aqueduct: BARRINGTON, Brain, 1928.

[2]) F. H. LEWY. Die Lehre vom Tonus und der Bewegung, eine systematische Untersuchung zur Klinik etc. der Paralysis agitans. Springer, Berlin, 1923.

The cortex.

In Cyclostomes and Plagiostomes the structure of the caudal part of the mantle differs from the pallial centers of the olfactory tracts or *palaeocortex*. The more caudal part, JOHNSTON's and HOLMGRENS primordium hippocampi, may be a primitive *archicortex* (p. 97).

In Amphibia two distinctly different areas are found, laterally the *palaeocortex* and medially the *archicortex*, the former receiving only olfactory tract fibers, the latter chiefly tertiary olfactory impulses.

In the palaeocortex all cells lie very near the ventricle (fig. 69), extending their dendrites peripherally to the unmyelinated olfactory tracts that run in the superficial layer of the pallium. In the archicortex the cell bodies themselves have migrated in the direction of the superficial fiber layer, which is much stronger here than in the palaeocortex, and is moreover medullated. This migration apparently is a process of *neurobiotaxis* (KUHLENBECK) [1]).

A further differentiation occurs in *Reptiles*, especially in Lizards and Serpents, where three distinct cortical layers are seen (fig. 77), a lateral, dorsal and medio-dorsal layer. The first and second consist of larger cells, the latter is made up of small granular cells.

The frontal part of the lateral layer receives olfactory tract fibers. It thus represents the oldest or *palaeocortex* (primitive praepiriform cortex in BRODMANN's nomenclature).

Caudally this cortex passes into the piriform cortex, which, however differs only slightly from the praepiriform cortex in these animals (cf. CROSBY and ROSE). Medially it is connected with the archistriatum.

The dorsal and medio-dorsal layers form together the *archicortex* or hippocampus, which, also in mammals, consists of two layers.

The dorsal layer represents the *ammonpyramids* and the medio-dorsal or granular [2]) layer the *fascia dentata* (ADOLF MEYER).

The relation between the fascia dentata and the ammonpyramids is such, that the latter, for a short distance, extend underneath the former, thus, in part, becoming subgranular (fig. 77, superpositio medialis [3])).

---

[1]) Ueber den Ursprung der Grosshirnrinde. Anat. Anzeiger, Bnd. 55, 1922.

[2]) Some large pyramidal cells occur more dorsally, at the lateral edge of the fascia dentata, which extends upward, changing its granular character into a pyramidal character. Probably these cells send out association fibers. They are, however, few.

[3]) Laterally it extends under the palaeocortex: superpositio lateralis.

The functions of these two archicortical layers are different. The granular layer, or fascia dentata, has only small cells, whose neurites arborize for the most part in the neighbourhood (some in the septum).

It has a *receptive correlative function*, receiving tertiary olfactory and some visceral fibers (from the tweenbrain, CROSBY). The neurites of the ammonpyramids, however, descend to the thalamus (in the
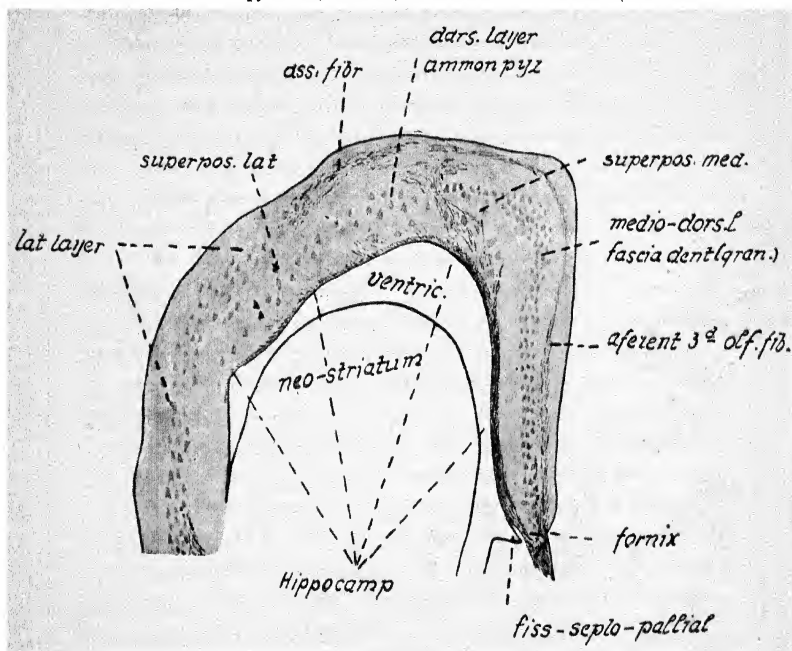
Fig. 77. Forebrain cortex of a serpent compare with this fig. 78.

taenia thalami and fornix). These cells consequently have an *efferent function*. In addition they form the comm. pallii or psalterium.

In Reptiles we do not find any structural equivalent to the mammalian neocortex, i. e. a cortex consisting of several (five) cell-layers, one lying on the top of the other.

But there may be a *primordium neopalli*, as ELLIOT SMITH called it, or *general cortex* (CROSBY), in an undifferentiated way.

In order to find out if such a primordium neopallii exists in Reptiles, we must ask whether there are any fibers coming from the neo-

thalamus that terminate in the cortex, since the typical feature of the neocortex is its receiving of neothalamic projections.

This seems to be case in Varanus.

As was mentioned above, in this animal a strong tract runs from the neothalamus to the neostriatum (fig. 72).

Some of these fibers, however, do not terminate in the neostriatum, but may continue in the mantle, ending (some perhaps originating) in cells that are contiguous with the dorsal edge of the lateral cortex. These cells thus lie between the palaeo- and archicortex. So if there is a primordium neopallii, it is located in a region connected with, and perhaps arising from the dorsal edge of the palaeo-cortex, in the frontal region of the mantle (see fig. 72).

Now this is very interesting, since we know that the mammalian neocortex is also located between the palaeocortex or cortex lobi olfactorii, and the archicortex or hippocampus (fig. 78).

Whereas in mammals, even in the lowest (OBENCHAIN) the neocortex is larger than the other forms of cortex, and also much thicker, it is a mere trace in reptiles, characterized only by this fiber connection and by a slight thickening of the mantle, about the level where the neostriatum comes into contact with it (fig. 72).

Consequently, a first vestige of a neocortex, if present in reptiles, occurs only in the frontal part of the mantle, lying between the archicortex and palaeocortex, and contiguous with the latter.

Another argument in favor of the conception that the neocortex arises from a primordium contiguous with the palaeo-cortex, is the fact that the neocortical commissure, the callosum, where it first occurs, in Monotremes, runs with the palaeocortical commissure (comm. anterior), and not with the archicortical (the psalterium).

In *mammals* the great development of the neocortex has pushed the palaeocortex, which here has differentiated in a superficial granular and a deep pyramidal layer, ventrally, producing a deep groove, the *fiss. rhinalis* (fig. 78), a *limiting fissure*.

On the other hand, the dorso-medial outgrowth of the neocortex causes the archicortex to be lifted up in a dorsal and medial direction, thus producing its semicircular form, the lower edge of which contains the fascia dentata, whilst the curve itself contains the ammonpyramids (fig. 78 and 79).

The infolding of the archicortex gives rise to an *axial fissure*, on the mesial surface of the mantle, the *fissura hippocampi*.

The function of the granular fascia dentata remains the same
as in Reptiles, being receptive correlative. Similarly, efferent (taenia,
fornix) and commissural fibers (psalterium) arise from the ammon-
pyramids.
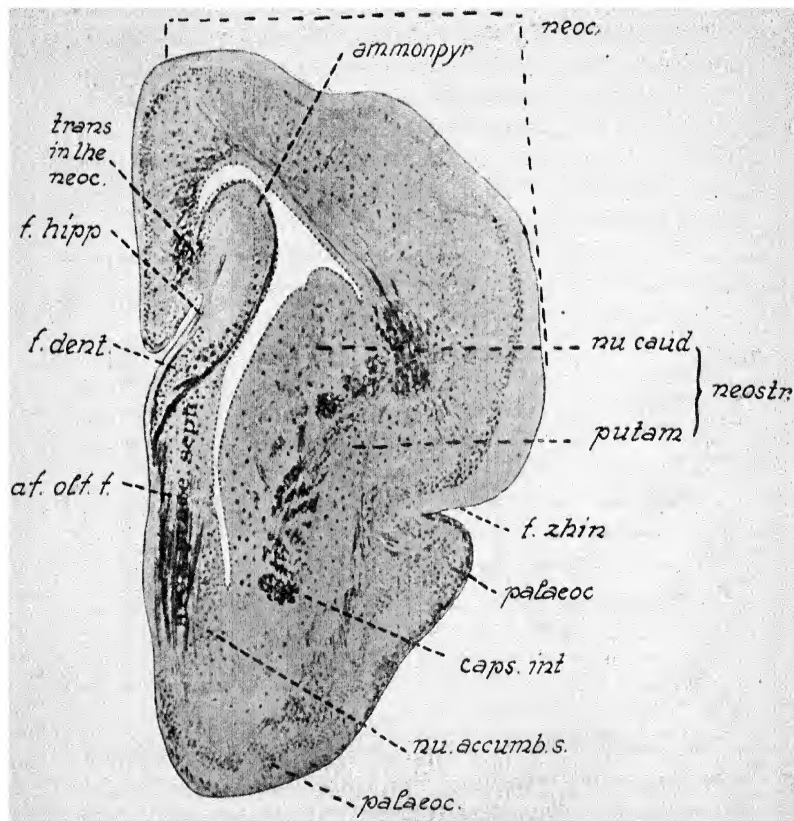
Fig. 78. Section through the frontal part of the forebrain of Hypsiprymnus
rufescens. Note the location of the neocortex between the archicortex or
hippocampus [1]) and palaeo-cortex.

The *neocortex* in mammals is not only larger, but also thicker
than the palaeo- and archicortex. Its thickness is chiefly due to the

---

[1]) This is sometimes called hippocampus major in contradistinction to the
calcar avis, the protrusion of the fissura calcarina in the cornu posterius of
the lateral ventricle in primates that is sometimes called hippocampus minor.

fact that, in addition to an increase of the subgranular pyramids, a large amount of *supragranular cells* develops here, which stop at the level of the fiss. hippocampi (fig. 79).

In the neocortex six layers occur (BRODMANN; cf. fig. 80): I. zonal-
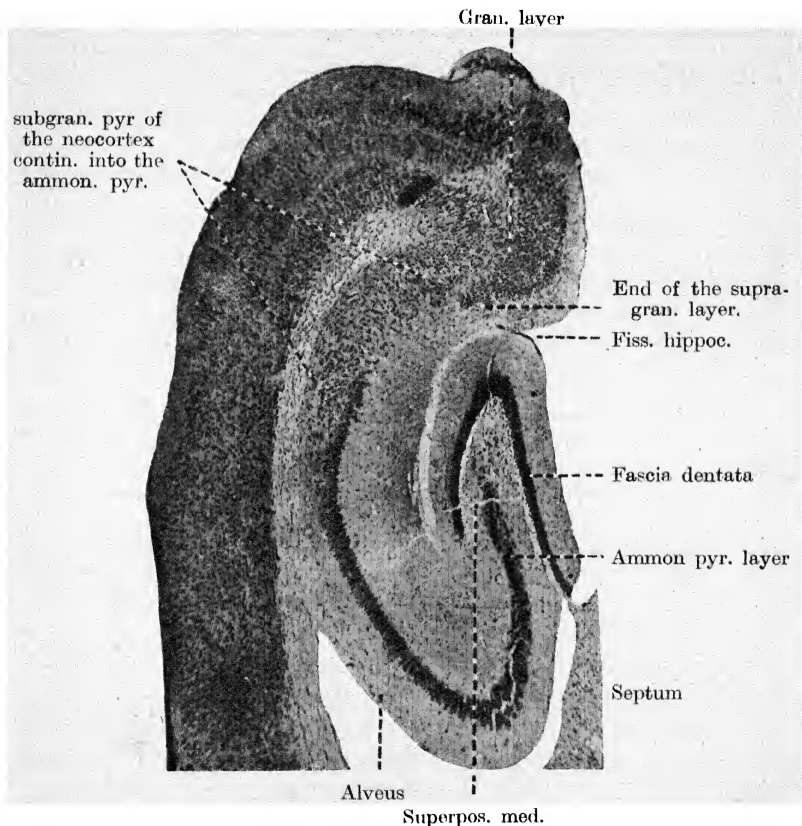
Fig. 79. Rat. Transition of the ammon pyramids in the deep cell layer of the neocortex.

or tangential layer (which is not cellular), II. layer of small pyramidal or stellate cells, (also called granularis externa); III. the large supragranular pyramids, IV. the (internal) granular layer; V. lamina ganglionaris and VI., the multiform layer. As we shall see, the five cellular layers may be divided into three groups: the supragranular (II, III) granular (IV) and subgranular (V, VI) layers.

While the granular layer of the neocortex is the homologue of the granular layer of the archicortex and palaeocortex and its sub-granular pyramids are homologous (also functionally) with the subgranular pyramids of the palaeo- and archicortex, in which they even continue (fig. 79), *the supra-granular pyramids of the neocortex are a new feature, characteristic of the neocortex only.*

The receptive correlative function of the granular layer in the neocortex appears from the fact that it is most developed in those areas that receive many impulses (visual, sensory, auditory and frontal area), while the subgranular pyramids also in the neocortex give rise to cortico-fugal (HOLMES, NISSL, BIELSCHOWSKY) and commissural fibers (v. VALKENBURG, LORENTE DE NO).

The supragranular pyramids develop at the expense of the granular cells (VAN 'T HOOG) and like these are receptive correlative, but the correlative or *associative* function prevails. The receptive function appears e. g. from the fact that in the visual area the supragranular cells are atrophied after long lasting blindness acquired in youth (LEONOWA, HENSCHEN, BERGER, LENZ, KLEIST).

That this layer practically is an (associative) extension of the granular layer (IV), was proved by VAN 'T HOOG, who demonstrated that between animals of the same order which differ in size (as cat and tiger, sheep and cow), the larger animal always shows an increase of the supragranular at the · expense of the granular layer.

That the effectory subgranular layer increases less is due to the fact that in the larger animal the sensory innervation increases with the muscular mass (proprioceptive sense) and surface (cutaneous sense), while the motor endings increase with the muscular mass only.

The specific associative nature of the supragranular layers, results from the fact that they receive the endbranches of callosum [1]) and homolateral associative fibers (VAN VALKENBURG) and also from the fact that they are more developed (MOTT, VAN 'T HOOG) in higher than in the lower Mammals and the last to differentiate ontogenetically (BOLTON, BRODMANN). In extreme idiocy it may be more arrested (BOLTON) than the granular and subgranular layers.

Cells in the supra- and subgranular layer (but especially in III) are not rarely degenerated in dementia praecox (ALZHEIMER, VOGT, JOSEPHY, K. H. BOUMAN), which is explained by BOUMAN, by a lack of vitality of these layers in such cases, an explanation that well agrees with MOTT'S conception of this disease.

---

[1]) According to *Lorente de No* they also give origin to a part of the callosum.

Fig. 80. Some of the chief areae of the human neocortex. Drawings by VAN 'T HOOG.

Frontal area (cerebellar prrojections).

Praecentral area. Motor area.

Postcentral area. Sensory area.

Temporal area. Acustic area.
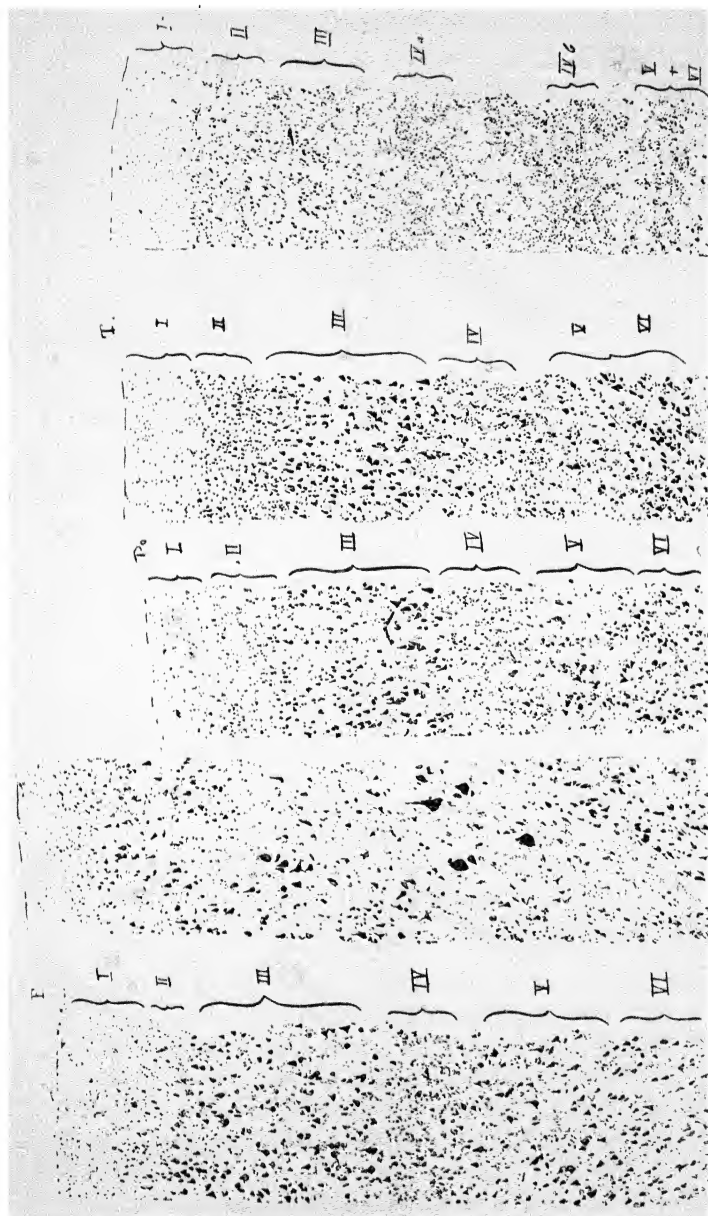
Occipital (striate or visuo-sensory) area.

I shall not deal further with the functional character of the three principal cell layers of the neocortex, as, since I defended this first (1908) it has been corrobarated by the work of several authors (JAKOB, VALKENBURG, BIELSCHOWSKY, KUHLENBECK, ECONOMO).

It seems to me that the sub-division of the supragranular cells into two strata (II and III of BRODMANN), and that of the subgranular cells into two strata (V and VI of this author) is not of such a fundamental importance as the principal division just mentioned.

The division in three principally different strata holds good for all the areae of the neocortex, with the exception of the motor (praecentral area), where the granular layer nearly entirely dissolves in pyramidal cells (see fig. 80).

It is, however, not strange, considering the different functions of these layers, that their relative diameter and compactness vary considerably, according to the character of the prevailing function of the field. So the associative supragranular layer is most conspicuous in those areae that have many associative connections: the frontal, praecentral, temporal, and visuo-psychic area, while in the frontal, sensory, auditory, and visuo-sensory cortex, that receive a great many subcortical projection fibers, the granular cells are very abundant, this layer being even doubled in the visuo-sensory area of primates and man (see fig. 80).

On the other hand, the deeper (subgranular) efferent pyramids are most developed in the praecentral or motor area of the brain (BETZ' cells, see fig. 80).

The cytotectonic differences are connected with differences in the distribution of the fibers. Both lead CAMPBELL to map out various regions of the neocortex, a work in which BRODMANN, FORTUYN, ECONOMO and KOSKINOS [1]) (for the cyto-tectonic division) and the VOGTS and their pupils for the fiber arrangement (myelo-tectonic division) have excelled.

The myelotectonic division, recently made by the VOGTS, has given a still more detailed differentiation. It has, however, appeared that the chief neocortical regions are present from the lower to the higher mammals, though differing greatly in extent and subdivision. Only the frontal region does not occur in the lowest, and this, and the parietal, post-temporal and visuo-psychic (peri-

---

[1]) Die Cytoarchitektonik der Hirnrinde des erwachsenen Menschen, Berlin 1926.
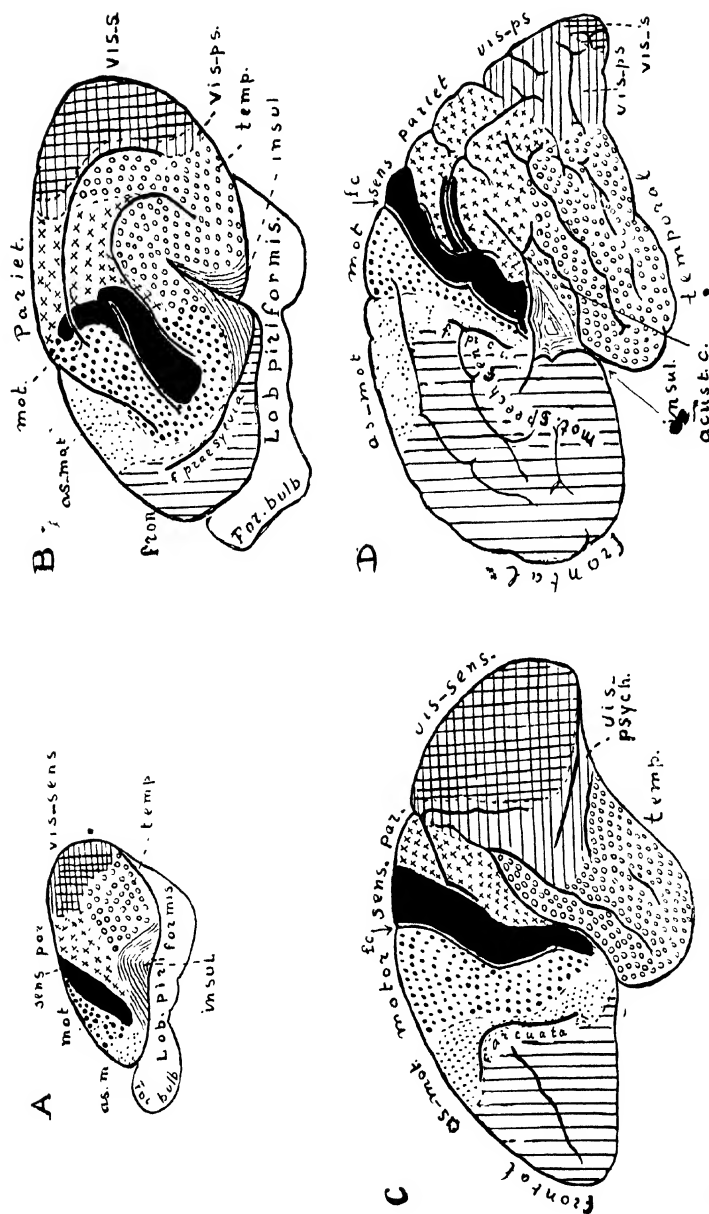
Fig. 81. Cortical regions in Spelerpes (A), Cercoleptes (B), Cercopithecus (C) and Homo (D), after BRODMANN. Black = sensory; big dots = motor; small dots = associative motor; vertical lines = kinaesthetic and behaviouristic; crossed = stereognostic; squared = visuo-sensory; horizontal lines = visuo-psychic; open circles = temporal; and concentric lines = the insular region (not indicated in C).

striate) regions are those that increase most in primates (see fig. 81).

It is interesting that the increase in extent of these regions (especially of the frontal region) also appears from comparative studies on fissuration (CUNNINGHAM, ELL. SMITH, ZIEHEN and others), although, of course, not in such an exact way as is shown by the comparative cytotectonic work of BRODMANN and others.

Careful comparisons or fissural anatomy and cytotectonic relations in the different orders of mammals, have enabled me to confirm these observations.

I have, however, been struck by the singular fact, that the progressive development of a cytotectonic area appears, nearly always, to be somewhat larger than might be expected from comparative fissural studies alone. In other words, the shifting of the fissures follows the differentiation of the brain mantle slowly; the fissures are, in a way, more conservative than the cytotectonic fields.

Fig. 81, made after BRODMANN's results, shows the cytotectonic fields in a rodent (Spelerpes), a bear (Cercoleptes), a monkey (Cercopithecus) and in man. The enormous increase of the frontal, posttemporal and parieto-occipital regions in primates, especially in man, is striking.

These regions which, phylogenetically, are apparently newer than the so called projection areas of the cortex, are also the latest to develop their myeline sheaths in the new-born child, as appears from the myelogenetic researches of FLECHSIG (fig. 82), which, in this respect, have been confirmed by the VOGTS.

It is, however, wrong to consider these regions as only associative in character, as FLECHSIG originally did. Like the other cortex fields they have also subcortical connections. But, the subcortical centers with which they are connected are more recent developments, and much larger in the higher than in the lower mammals. Moreover, these subcortical centers themselves for the most part are correlation centers.

So the frontal cortex receives (nucleus ruber) and emits (pons) cerebellar correlations. The frontal cortex thus influences finer adjusted actions, and behavior in general.

Also the motor speech center in man forms a part of it (directly in front of the insula), while the most frontal portion seems to influence general behaviour. Degeneration of the latter causes great behavioristic changes. Also the post-temporal region is doubly connected with the cerebellum, in the same way as the frontal

cortex. The parieto-occipital area on the other hand is connected with the pulvinar thalami, a stereognostic correlation centre.

So, though intra-hemispheric associations are abundant in these
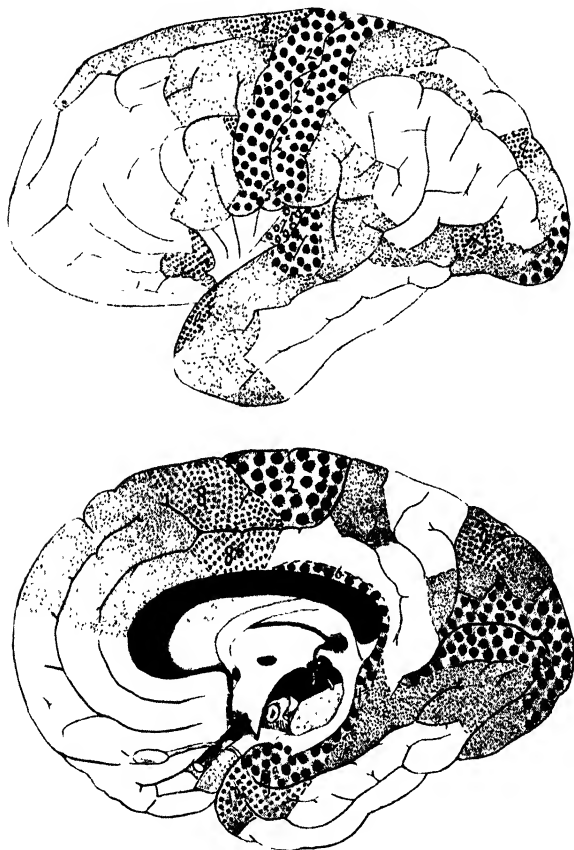
Fig. 82. Myelogenetic areas of the human cortex. The large dotted areas myelinate first, the small dotted next, then the grey areas, and finally the light ones, which are the frontal, posttemporal and parieto-ooccipital areas. After FLECHSIG.

cortical regions, their special character largely depends on the correlative character of their subcortical centers.

The other cortical projections arise from thalamic nuclei whose functions probably are less complicated.

EVOLUTION OF THE BRAINSTEM.

The thalamus.

This leads us to consider the progressive evolution of the brain stem in mammals, especially the thalamus and midbrain, where
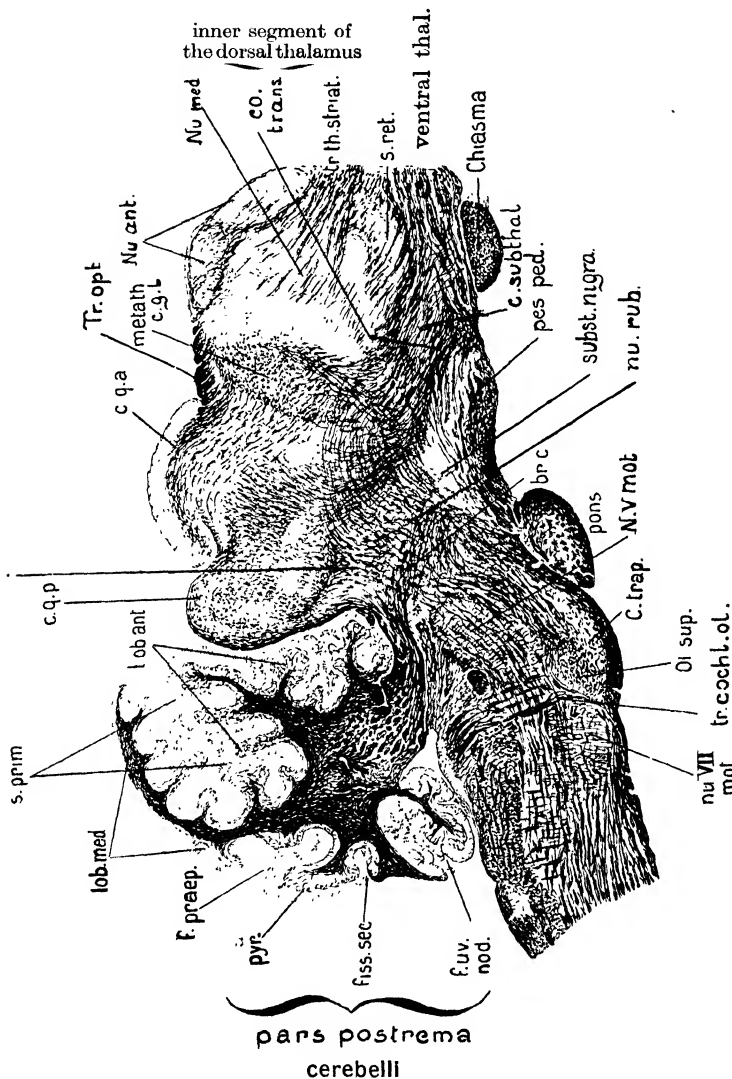
Fig. 83. The brain stem of a Marsupial, Onychogale frenata, showing the large size of the inner segment of the dorsal thalamus (nucl. anterior and nucl. medio-ventralis).

the new cellgroups arise, which are connected with the neo-striatal and neo-cortical development mentioned above.

Concerning the nuclei connected with the striatum I may be short.

Its oldest part or palaeo-striatum in all animals is connected with, the ventral thalamic and basal mesencephalic regions — the corpus hypothalamicum (LUYS), substantia nigra (peduncular nuclei of lower vertebrates) and nucl. ruber, in an ascending, but chiefly descending way (extrapyramidal motor system; F. H. LEWY, FERRARO, SPATZ).

The neostriatum increases with the development of the *inner segment of the dorsal thalamus*, the nuclei anterior and medio-ventralis (fig. 83).

The *development of the neopallium* in mammals and its increase in the higher orders of this class, especially in primates and in man, is mediated, chiefly, by the development of the *lateral segment of the dorsal thalamus* (fig. 84), and some parts of the midbrain, and depends largely on the higher development of vision, hearing, stereognostic sense, and precision of movement.

As in reptiles practically no real neocortex occurs, but only a neostriatum, the further differentiation of the dorsal thalamus in these animals is limited practically to the anterior and medial nuclei and a small nucleus ventralis, all connected with the neostriatum. In mammals, however, not only do these nuclei but also the nuclei of the lateral segment enlarge; the geniculate ganglion increases and new projection centers appear, as the lateral thalamic nucleus and the pulvinar. In the midbrain the medial geniculate nucleus appears and the nucl. ruber enlarges considerably as a center of cerebellar projections to the cortex (and striatum).

The increase of the *lateral geniculate body*, especially in primates, is due to the greater number of optic fibers, not merely collaterals as in the primitive geniculate of fishes, but actual terminations of the optic tract in this nucleus. On the other hand the tectum opticum, corpora quadrigemina anteriora, as it is called in mammals, correspondingly receives less optic fibers and thus diminishes in size.

The geniculate body becomes the projection nucleus of visual impressions on the cortex, whereas the corpora quadrigemina anteriora only retain a function for the elaboration of visual reflexes.

This growth of the geniculate is influenced by the development of binocular vision in mammals in general, and of macular vision in the higher mammals, starting with Carnivora.

While in fishes, where only panoramic vision occurs, the optic nerves hardly collaborate and totally decussate on their course to the midbrain roof (fig. 85), macular vision of mammals causes the temporal retina of one eye to collaborate with the nasal retina of the other, and, consequently, causes temporal fibers of one eye to run with nasal fibers of the other (fig. 86), *a neurobiotactic consequence of the fact that the lateral half of one eye cooperates simultaneously with the medial half of the other*, as do the corresponding parts of the statocysts of Pterotrachea (cf. fig. 86 with fig. 26 and p. 45).
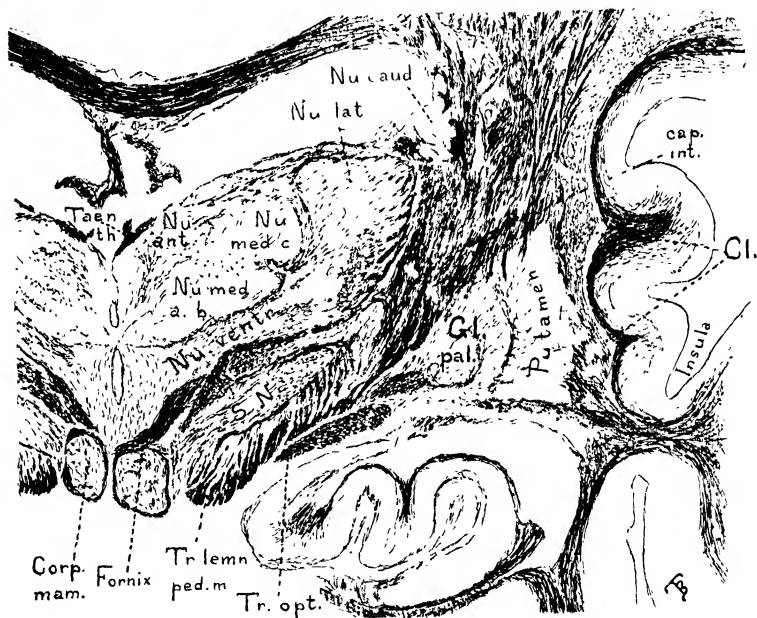
Fig 84.

Transverse section of the human tweenbrain and adjacent parts, showing the enormous increase of the dorsal thalamus, specially of its lateral segment (nu. lat.), connected with the cortex by the caps. interna.

So each geniculate body receives fibers of *both eyes* and among them a great many macular fibers of both eyes.

On the other hand, the midbrain remains a crossed center, as in lower vertebrates, each half of it receiving fibers of one eye only.

In Primates the geniculate cells are arranged in parallel rows,

alternatingly connected with the left and right eyes (MINKOWSKI).

Another localization in the geniculate body has been demonstrated by BROUWER and ZEEMAN, who studied the projection of the retinal quadrants in the geniculatum and on the visual cortex.

In the rabbit, the projection of the retina on the geniculatum is such that its dorsal quadrants lie ventrally in the geniculatum, the ventral quadrants dorsally, thus being exactly reversed. The same holds good for the outer and inner quadrants.

In monkeys, however, the superior quadrants of the retina are projected laterally on the corp. geniculatum, and the lower quadrants
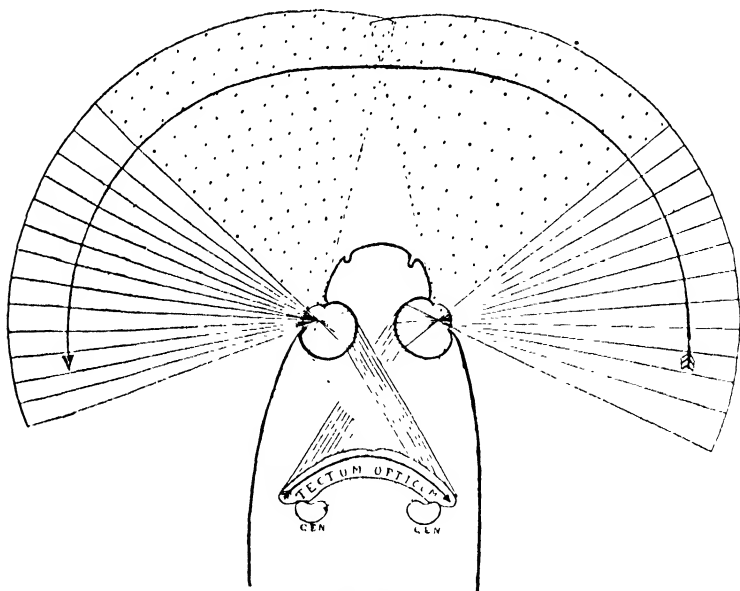
Fig. 85.

Panoramic vision in this Teleost does not involve collaboration between the temporal retina field of one eye and the nasal retina field of the other.

medially. This difference is to be explained, by the turning of the geniculate body in these animals, in a consequence of the pressure of the enlarged pulvinar.

The macular fibers — very numerous in Primates and in man —, are projected in the middle and each geniculatum receives macular fibers of both eyes. As these fibers are very numerous,
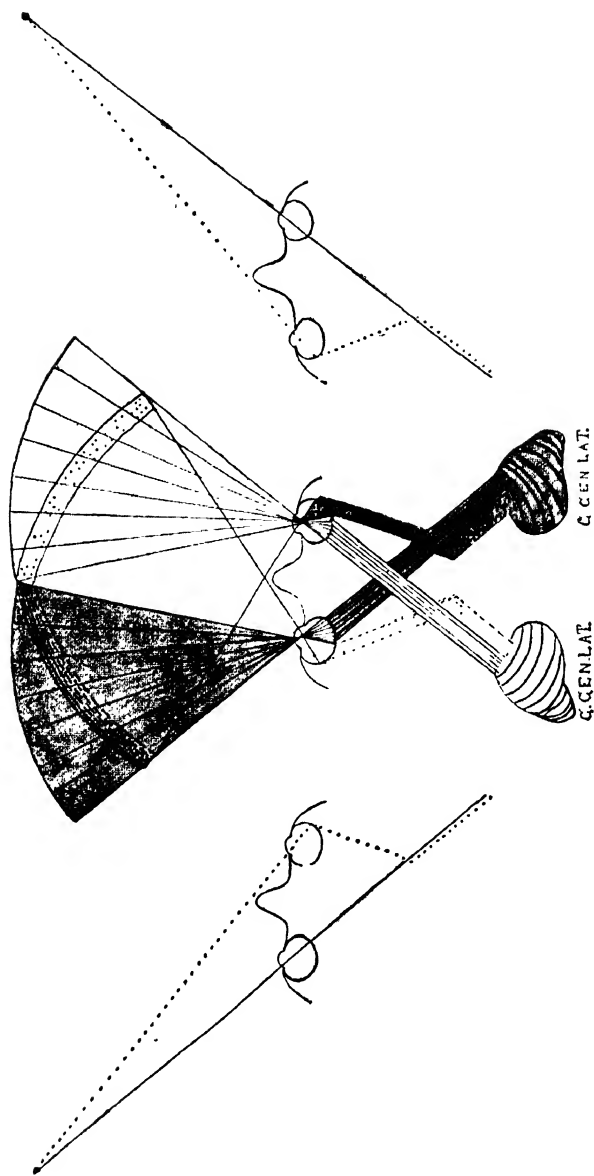
Fig. 86. To explain the optic semi-decussation in mammals. The visual field of the temporal retinal area (dotted) of one eye collaborates with the visual field of the nasal retinal area (striped) of the other, thus causing the temporal fibers of one eye to join the crossed nasal fibers of the other and consequently to run homolaterally (cf. the static semidecussation in Pterotrachea, fig. 26).

the area they occupy overlaps that of the non-macular projections (BROUWER and ZEEMAN) as probably also occurs in the cortex [1]).

In the cortex the ventral retinal quadrants are represented ventrally, the dorsal dorsally (PUTNAM, rabbit) in the area striata, which in some lower mammals and in primates shows a double granular layer (BRODMANN).

The cortical projection of the macula extends more laterally on the convexity than the non-macular projection (BROUWER, ZEEMAN).

The lateral geniculatum also receives fibers from the visual cortex (PROBST [2]), BOUMAN [3]), BROUWER [4])), as do the corp. quadrigemina anteriora (BOUMAN [3])).

The *medial geniculate body* is related to the posterior corpora quadrigemina in a similar way as the lateral geniculata to the anterior quadrigemina. The posterior quadrigemina develop from the tori semicirculares of the lower vertebrates (see fig. 62), which beginning with Amphibia, also receive auditory impulses, while in fishes the tori semicirculares receive only lateral line and vestibular impulses [5]).

In mammals the cochlear impulses of each ear are projected on the cortex of both temporal lobes (MOTT) in the auditory center of FLECHSIG (field 7 in fig. 82).

Similarly from the *ventro-lateral* and *lateral thalamic nuclei* cortical projections of skin and muscle sensibility originate.

The cutaneous and proprioceptive sensibility localized in these nuclei is of a higher order than the primitive skin and muscle perceptions which prevail in fishes, and there are either elaborated in the cord, or in the cerebellum and midbrain. Their peripheral endings also differ.

In lower vertebrates the sensory neurones of the skin terminate chiefly as *simple endings*, or as anastomozing networks in the ordinary epidermis.

In the human body some regions still occur where the sensory nerves entirely, or nearly entirely, terminate in this way.

---

[1]) For further details I refer to BROUWER and ZEEMAN. Experimental and anatomical investigations concerning the projection of the retina on the primary optic centers in apes. Journ. of Neurology and Psychopathology, Vol. VI, 1925.

[2]) PROBST, Arch. f. Psychiatrie und Neurologie, Bnd. 35, 1902.

[3]) K. H. BOUMAN, Inaugural dissertation, Amsterdam, 1905.

[4]) BROUWER, Proceed. Kon. Akad. v. Wetensch. Amsterdam, Vol. 31, 1928.

[5]) The sacculus of the labyrinth in some fishes is, however, (PARKER) sensitive to primitive sounds.

Such parts are the cornea of the eye, the gingiva of the teeth, the surfaces of the intestine.

The skin and subcutaneous tissue of higher animals and man, contain, however, *special nerve endings*, terminating in *complicated terminal bodies*, such as the sensory corpuscles of MEISSNER, (cutaneous sense), PACINI, (deep sense) and other terminal corpuscles.

Such corpuscles are to be found throughout the skin, but the tips of the fingers and the inner side of the hands in particular are richly provided with some of these corpuscles.

If we now compare the sensibility of such surfaces as the cornea, gingiva or intestine with those of the hand and fingers, we find that the former is nearly entirely restricted to recognition of pain, a poorly localized perception of touch and tension, and the distinction of temperatures below 26° C. and above 37° C.

Apparently these are the most *primitive sensations*. They are the first to develop in the lower animals, as they are also the first to reappear after nerve section in man, as HEAD and SHERREN showed.

HEAD has termed these sensations *protopathic* because they are the first (*protos*) to appear, and because they usually produce an affect (*pathos*). We may also call them: *vital sensations* (FABRITIUS), as they have to do with the first vital exigencies, such as escape from noxious [1]) influences (nocireceptive endings of SHERRINGTON).

PARSONS [2]) has called them *dyscritic* sensations, because they do not perceive small differences of sensation. On the contrary, the sensibility of the surfaces that are richly provided with special corpuscles is of a higher order, and perceives very slight changes in the stimulus and its localization. Thus, minute characteristics of objects may be recognized with closed eyes. HEAD called this the *epicritic sense*. We may also name it the *gnostic sense,* as the increase of our knowledge of the surrounding objects largely depends on it.

To this fine cutaneous sensibility a highly developed subcutaneous (deep) sense, chiefly muscle and joint sense, are added, giving exact information about the position of the extremities and joints (stereognostic sense).

---

[1]) They are, however, not only related to noxious, but also to some agreeable feelings, so that they are also partly gratoreceptive (KAPPERS).

[2]) PARSONS. An introduction to the theory of perception. Cambridge Psychological Library 1927.

As I pointed out elsewhere this evolution of sense also holds good for special sense organs, as the labyrinth and eye. So the first function of the labyrinth is maintainance of equilibrium, a highly vital function, and the first function of the simple eyes of lower invertebrates is the appreciation of the quantity, quality and direction of light, equally of vital importance. The auditory function of the labyrinth, as the perception of images in the eye appear later in phylogeny and have a more gnostic character (cf. also PARSONS).

The development of this highly developed skin sensibility and stereognostic sense causes the sensory spinal roots to increase, and to develop, in addition to short descending (reflectory) branches, long *ascending dichotomizations* that accumulate frontally, forming the *posterior funiculi*, which terminate near the oblongata in the *nuclei gracilis* (GOLL) and *cuneatus* (BURDACH). Still small in reptiles and birds the nuclei of the posterior funiculi increase in mammals together with the posterior funiculi, and attain their largest size in primates and in man (BROUWER, ZEEHANDELAAR).

From here, their impressions are transmitted by the *mesial fillet* to the ventro-lateral thalamic nuclei, being joined in the oblongata by an analogous tract from the *frontal sensory V nucleus* (cf. p. 164) that terminates in the ventro-medial nuclei of the thalamus (WALLENBERG, WINKLER).

From the thalamus they run to the post- and praecentral cortex.

This projection takes place in such a way that the gnostic sensations of the skin are transmitted to the postcentral, the deep or proprioceptive sensations to the praecentral cortex, where the *motor cortical* or *pyramidal tracts* originate (see further p. 171).

So vision, hearing, cutaneous and deep sensibility have their own thalamic centers. But they are also mutually connected either by short neurones between their thalamic centers or by special thalamic nuclei that only serve *intra-thalamic correlations* (INGVAR).

The *pulvinar thalami* seems to be such a nucleus. It lies between the anterior thalamic nucleus and the lateral geniculate body. Still small in the lower mammals, it increases rapidly in the higher ones, and, in primates and in man, acquires an enormous size.

The connections of this exquisite neothalamic center are not yet sufficiently known, but it seems certain that various impulses end in it, and that, moreover, it receives intercalary neurones from the lateral stereognostic nucleus, as well as from the geniculatum [1]),

---

[1]) The assertion that the pulvinar receives *direct* neurones from the optic

and even fibers from the cerebellum (HORSLEY and CLARKE) and nucleus ruber (WINKLER). These stereognostic correlations are projected in the parietal region of the cortex.

Thus, we see that the lateral segment of the neo-thalamus is an

Nu. cun. (Burdach)   Nu. grac. (Goll)   Nu. cun. ext.
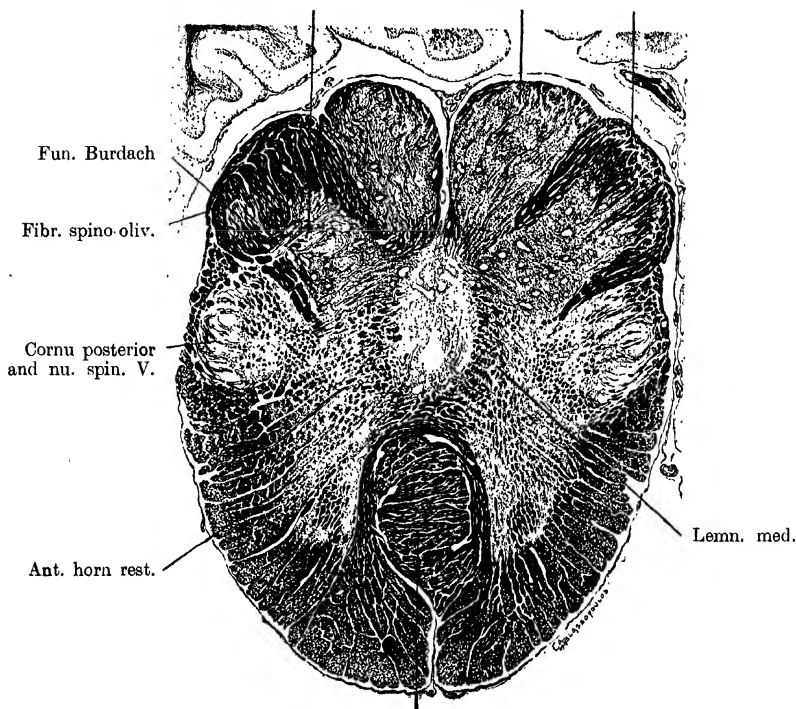
Pyramidal decussation.

Fig. 86. Section of the upper cervical region of the human spinal cord, showing the posterior funicular nuclei (of GOLL and BURDACH) which are wanting in fishes and amphibia (cf. fig. 51).

important synaps for gnostic sensations and correlations on their way to the cortex.

---

tract (BERNHEIMER, MONAKOW) has been contested by BROUWER on account of failing MARCHI degenerations, but LORENTE DE NO believes those end branches to be unmyelinated.

Also the midbrain base takes part in this function, by means of the *nucleus ruber*, which, — in·addition to the large cells of the *rubro-spinal tract*, occurring already in reptiles and birds — in mammals, especially in the higher ones, contains a great many smaller cells (v. MONAKOW) that project *cerebellar correlations* on the frontal and occipito-temporal cortex (LA SALLE ARCHAMBAULT), probably also to the striatum.

The character of this cerebello-rubro-cortical projection can be only understood after studying the further evolution of the cerebellum.

The cerebellum in amphibia reptiles, birds and mammals.

We have seen (p. 101) that already in fishes the cerebellum may acquire a considerable size, as a consequence of the connections of the auriculi with the large static nerves (nerv. vestibularis and N. N. laterales), and of the corpus or middle part of the cerebellum with the spinal cord, inferior olive, tectum and hypothalamus.

The spino- and olivo-cerebellar projections that are present in fishes are, however, not very considerable. In animals, that do not constantly live in water, as adult frogs (p. 126), the lateral line organs disappear, and also the tectal and hypothalamic projections are reduced. As the spino- and olivo-cerebellar tracts are still small in frogs, the amphibian cerebellum does not acquire a large size.

In all higher animals, however, in connection with the greater importance of the limbs and neck for posture and gait, deep sensibility acts a much larger part in the positional functions, and consequently the spino- and olivo-cerebellar projections increase, thus causing a greater development of the corpus or vermis cerebelli.

So in *reptiles*, the corpus cerebelli again increases, and the cerebellar nuclei first acquire an intracerebellar position (cf. p. 104), the neurobiotactic result of impulses reaching them from the Purkinje cells.

In turtles and crocodiles it is curved in the same way as in Plagiostomes, forming a closed sack, which, in the crocodiles, exhibits two furrows. In Lizards it is turned inside out, curving over the midbrain roof (for details see LARSELL'S recent work [1]).

Similarly the enlargement of the *avian corpus cerebelli* is chiefly due to the enormous increase of spino-cerebellar fibers in these animals, where the inferior olivary connections are also more numerous.

---

[1] The cerebellum of reptiles: lizards and snakes. Journ. of Comp. Neur. 1928.

In birds the spino-cerebellar fibers, which in fishes only originate from the cervical cord, arise over the entire length of the cord (INGVAR). They end chiefly in the anterior and posterior thirds of the cerebellar body (fig. 87; for the physiology of these parts, see BREMER [1])). The pars media does not receive spino-cerebellar fibers, nor do the lingula, nodulus and flocculus (INGVAR).

The nodulus, lingula and flocculus (the homologue of the auriculus) also in birds, are connected with vestibular centers and in an efferent way with the eye muscle nuclei.
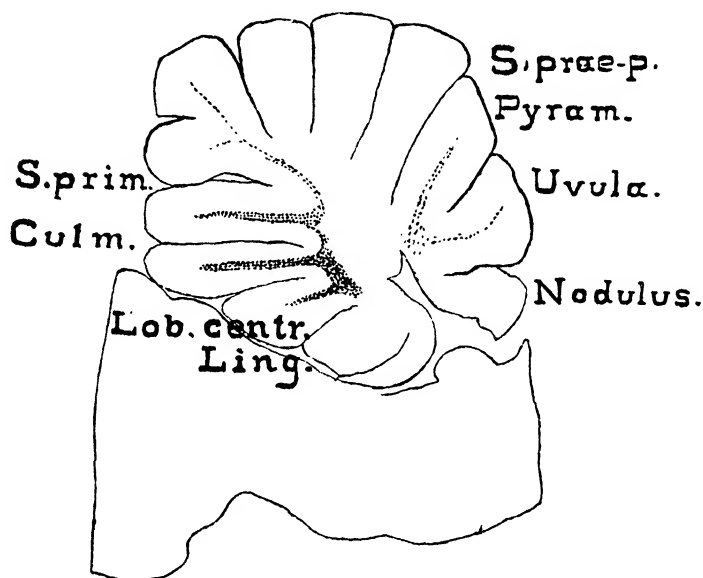
Fig. 87. Ending of the spino-cerebellar fibers in the pigeon (after INGVAR). In mammals the relations are similar.

Especially in *mammals* the corpus cerebelli (= *vermis*) receives a great many spinal and olivary impulses. In these animals, however, also impulses from the forebrain reach the cerebellum, via the *pons nuclei*, the cells of which originate in the static area of the oblongata (ESSICK, KOOY), but later acquire a ventral position.

---

[1]) BREMER, Recherches sur la physiologie du cervelet chez le pigion. Co. rendus de la Soc. de biologie, Tome 90, 1924.

The pons nuclei receive fibers from the frontal and temporal cortex and thus transmit neocortical viz. highly correlated impulses. This new connection causes a bilateral outgrowth of the vermis: the *cerebellar hemispheres* (fig. 88) or *neocerebellum* (EDINGER).

Whereas the spinal fibers are restricted to the same parts of the vermis as in birds, the pontine fibers spread over the whole vermis as well as over the cerebellar hemispheres, including the paraflocculus (fig. 89), as is especially obvious in whales (R. WILSON).

In addition, new inferior olivo-cerebellar tracts appear, terminating

fiss. prim.

lob. cer. ant.

lob. simplex

hemisph. cer.
(lob. ansatus)

pars media
vermis

tonsilla
(lob. paramed)

paraflocculus

fiss. praepyr.

uvula and nodulus
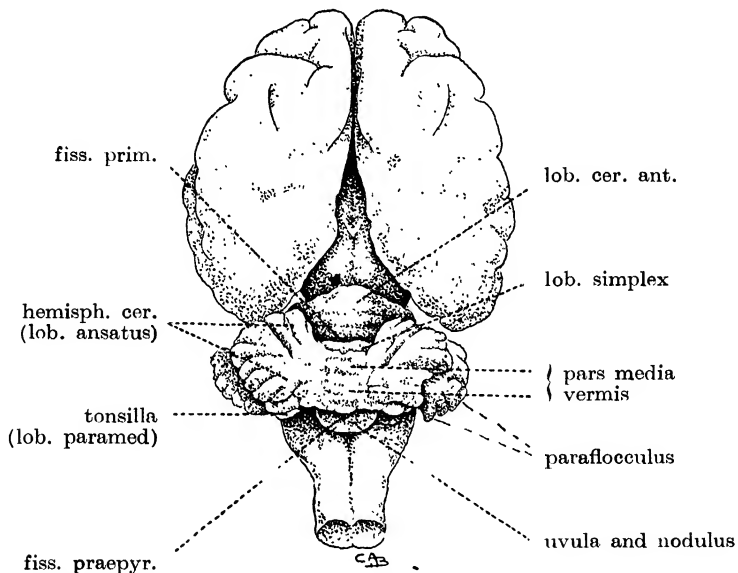
Fig. 88. The cerebellum and brain of a Marsupial, Phascolomys latifrons, showing the development of the cerebellar hemispheres from the middle part of the vermis.

also in the cerebellar hemispheres. These tracts originate in a new part of the olive, the *lateral olive*, which receives fibers, amongst others, from the striatum (WALLENBERG, WINKLER).

The medial olive, which is the older part (KOOY), receives fibers from the spinal cord (in fishes also from the tectum) and remains connected with the vermis cerebelli chiefly (HOLMES, BROUWER).

Thus the development of the cerebellar hemispheres in mammals, results from the fact that neo-cortical impulses reach the cerebellum
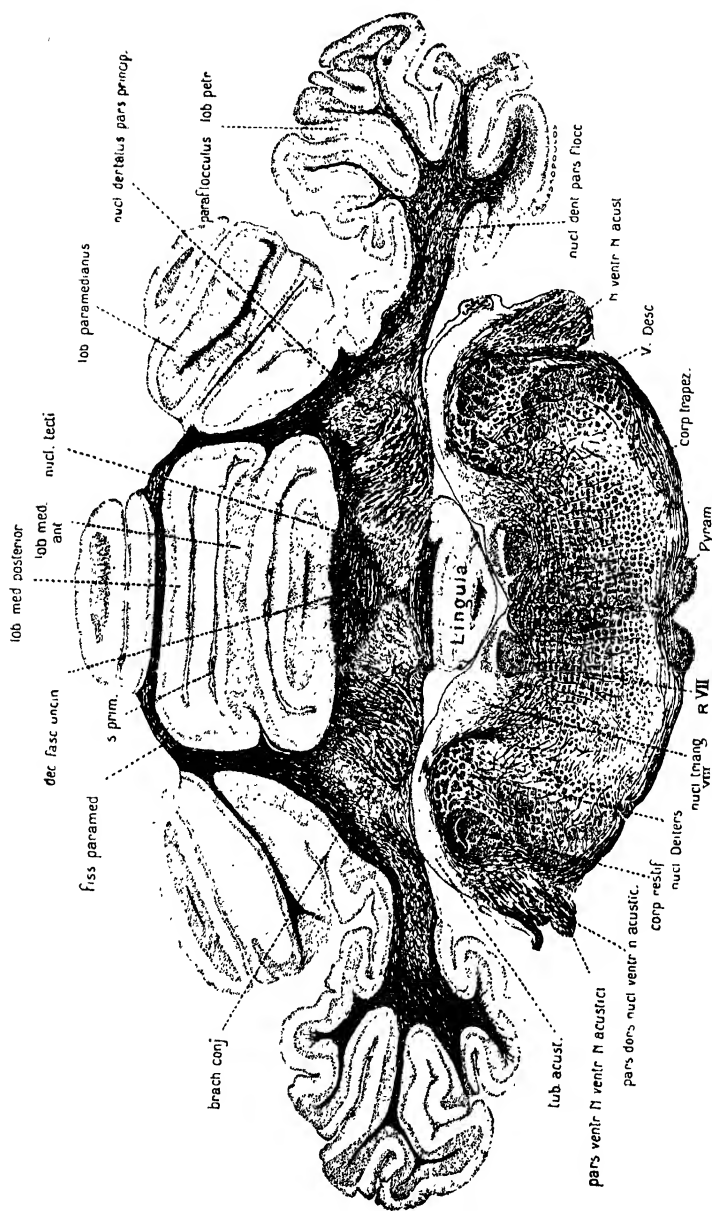
Fig. 89. Transverse section of the cerebellum of a rabbit. Note the large cerebellar nuclei: the nucl. tecti (or medialis) and the lateral dentate nucleus (pars principales and floccularis), from which the brachium conjunctivum to the midbrain arises.

in these animals by means of the pons, while at the same time, new striato-olivo-cerebellar impulses end in it.

Parallel with the development of these cerebello-petal impulses, the *efferent fibers of the cerebellum* become more numerous, especially those from the cerebellar nuclei (fig. 89) to the *nucleus ruber* of the midbrain.

This nucleus projects the impulses thus received to the frontal and temporal cortex and to the striatum, which, consequently are connected with the cerebellum in a descending as well as ascending way, both ways being crossed.

The double cortical connection increases in higher mammals, involving an enlargement of the cerebellar hemispheres, BOLK's *lobi ansati* and *paramediani* (fig. 88), which, small in lower mammals, become larger in Carnivora and attain a very great size in the Elephant, Edentates and Primates. Their development runs parallel with a more independant motility of the *extremities* (BOLK, VAN RIJNBERK, THOMAS).

The symmetric or alternating stereotype movement of the extremities and trunk (prevailing in reptiles, birds and lower mammals), remain connected with the vermis (BOLK), while a more free gait and more independent unilateral movements of the extremities, either in locomotion or in grasping, are connected with the development of the hemispheres.

The cerebellum influences these movements largely by *inhibition*.

INGVAR especially has emphasized that every bodily movement involves a certain amount of *inertia*, i. e. that each movement has a tendency to go on if it is not counteracted at a determined moment. Since a movement does not stop at once with the cessation of the innervation that causes it, it would only gradually decrease, if inhibition did not stop it exactly at the required place.

This inhibition is largely effected by prompt antagonistic action (BABINSKI, TILNEY and LEIRI). This is most evident if diseases of the cerebellum prevent its proper function.

In such cases prompt counteraction does not stop the inertia of movements. If, for instance, such a patient should intend to place his finger on his nose, his action does not stop at the required spot, but goes beyond its aim ("Vorbeizeigen" BARANY), or if somebody wants to stretch the patient's arm, while the latter keeps it strongly bent at its elbow joint, the patient's arm will — if the forced stretching suddenly ceases —, rebound very strongly (HOLMES' rebound phenomenon). Similarly quickly repeated movements with a sudden

stop between cannot be made (adiadochokinesis, BABINSKI). All these experiments show that the ability to stop muscle action immediately at the required moment by antagonistic innervation, fails in such cases.

So this cerebellar function evidently is of high importance in movements of finer adjustment, such as are involved in grasping objects and in independent movements of both arms as in handycraft, further in writing and speech. Consequently the cerebellum of higher mammals and the neocortical regions, specially the frontal region connected with it, are very important for finer stereopractic functions.

The bulbar centers in amphibia, reptiles, birds and mammals.

From the fact that the influence of the cerebellum is also evident in motor functions of the head (e. g. speech), it appears that not only the spinal proprioceptors are projected here, but also bulbar proprioceptive impulses.

This leads me to enter on the progressive changes in the bulbar centers, first of all, on those of the *sensory trigeminus root*.

The primitive sensory components of this nerve are simple proprioceptive and protopathic cutaneous.

In fishes most primitive proprioceptive fibers of the trigeminus run in the *radix mesencephalica* of this nerve, the intra-mesencephalic ganglion cells of which are equivalent to the intraspinal sensory ganglion cells (fig. 68). Peripherally this root runs with the motor branch, splitting up among the trigeminus muscles (WILLEMS).

The protopathic (dyscritic) fibers of the trigeminus descend, terminating in the *spinal fifth nucleus* (WOODS, BROUWER, ALLEN), where their impulses are elaborated in a reflectory way (e.g. cornea reflex), or projected on the midbrain (EDINGERS projection fibers).

These primitive proprioceptive and protopathic fibers remain in reptiles, birds and mammals, but, in addition to them, ascending epicritic (gnostic) dichotomizations develop (ALLEN), ending in the *frontal* sensory V *nucleus* (near its entrance) from which a crossed *trigeminal lemniscus* arises (WALLENBERG, LEWANDOWSKY, MONAKOW) analogous to the medial lemniscus and ending in the medio-ventral thalamic nucleus, whence its impulses are transmitted to the forebrain [1]).

---

[1]) From this sensory V nucleus in *birds* arises WALLENBERG'S *tr. quinto-frontalis* that ends in the forebrain base and palaeostriatum (see p. 131, 132).

The development of the frontal sensory V nucleus — which attains a very large size in mammals — is analogous to the development of the *nuclei funiculi posteriores* or nucl. of GOLL and BUR-DACH (fig. 86) for the ascending dichotomizations of the sensory spinal roots. Its projections, via the thalamus, are chiefly cortical.

From the same nucleus cerebellar projections arise, which, though occurring already in lower vertebrates, are much more numerous in birds (BIONDI, CRAIGIE [1])), and mammals (R. WILSON). Consequently the progressive development of this nerve is also in this respect similar to that of the spinal nerves (the more so since cerebellar projections arise not only from the posterior horns of the spinal cord but also from the nuclei funiculi posteriores (A. MUSSEN and YOSHIDA).

Whereas the trigeminus in mammals acquires connections with the forebrain cortex (and striatum), the connections of the *N. vestibularis* remain restricted to the bulb and cerebellum, the latter being connected with the vestibular nuclei in an ascending as well as in a descending way. The descending connection (*fasc. uncinatus*) arises in the nucl. tecti cerebelli chiefly and ends in the Deiters and descending vestibular nucleus (LEWANDOWSKY, BENDERS).

Thus, as far as concerns its vestibular part, the connections of the N. octavus do not exhibit principal changes in birds and mammals, although their nuclei are more differentiated (especially in the humming bird, CRAIGIE [1])) and their descending spinal tracts increase.

More conspicuous are the changes occurring in the N. octavus in consequence of the development of the *cochlea*, which, being absent in fishes, first arises in Amphibia, as an outgrowth of the sacculus. The cochlea is a new constituent that — in a way — may be considered as an gnostic addition to the more primitive and highly vital, reflectory acting semicircular canals, sacculus and utriculus (cf. p. 156, 157).

The *ramus cochlearis* — still very small in Amphibia — becomes greater in reptiles (BECCARI) and in birds (CAJAL) and in mammals even may acquire a larger size than the R. vestibularis.

---

[1]) CRAIGIE. Observations on the brain of the humming bird. Journ. of Comp. Neur. Vol. 45, 1928.

In birds this proprioceptive part of the frontal V. nucleus is even the largest and sends also crossed and uncrossed fibers to the striatum (WAL-LENBERG).

This increase of cochlearis fibers in mammals causes considerable changes in the size and position of their oblongata centers (KAPPERS).

The cochlear root of reptiles and birds ends in two dorsal nuclei, the *angular* and the *magno-cellular nuclei*, both lying at the extreme dorsal edge of the oblongata (fig. 90 A).

In mammals these nuclei increase in size and their arrangement changes, particularly that of the magno-cellular nucleus.

Whereas the chief change in the angular nucleus is its greater extension, forming the ventro-laterally extended *tuberculum acus-ticum* (fig. 90 B), the nucleus *dorsalis* magnocellularis changes

A. Section of the cochlear nuclei in Pratincola.

B. Section of the cochlear nuclei in the cat (FUSE).
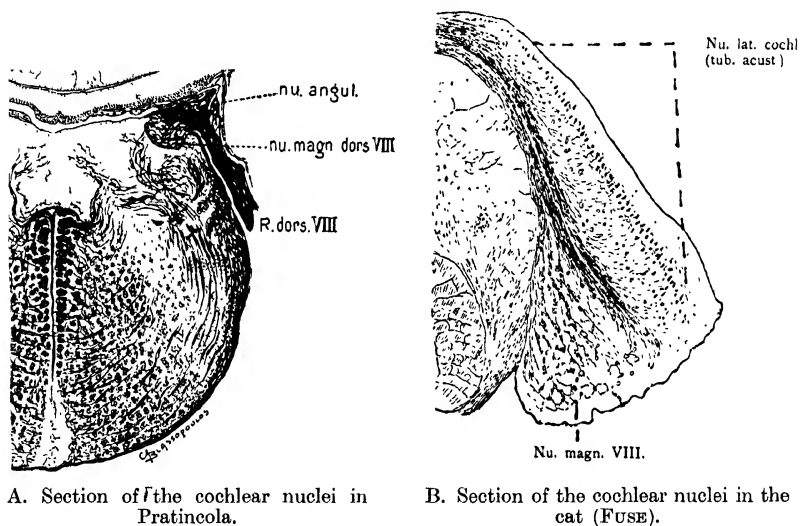
Fig. 90. The position of the cochlear nuclei in a bird and in a mammal.

its site entirely, shifting in the direction of the enlarging cochlear root. As the cochlea, from which this root arises, lies ventrally to the brain stem, this nucleus, approaching the entrance of its root, acquires a ventral position and in macroacoustic animals even bulges outside the oblongata.

This migration commences in Monotremes and Marsupials, where the nucleus still lies partly in a dorsal position (STOKES).

In mammals with a larger cochlea, such as rodents (fig. 89), carnivora (fig. 90 B) and primates, an almost entirely *ventral* position is attained.

It was formerly thought that this is due to the crowding of other structures in the oblongata of higher mammals, but that this is not so, is demonstrated by the fact that the most ventral position of the nucleus is not observed in primates, but in such animals as rodents [1]) and carnivora, where the oblongata is less crowded by new additions, but where the cochlea is larger than in man.

The migration of this originally entirely dorsal nucleus to a ventro-lateral position [2]) *is apparently effected by the neurobiotactic influence of the increasing cochlear impulses.*

These impulses are partly elaborated by the *superior olive* (Yoshida) [3]) partly transmitted by the *lateral lemniscus* to the corpora posteriora and medial geniculate body and hence projected on the temporal cortex (cf. p. 155).

The changes in the sensory roots of the *facialis, glosso-pharyngeus* and *vagus*, are far less striking. The chief difference with fishes is a reduction of taste fibers and an increase of general visceral fibers in connection with the development of the lungs. The atrophy of taste fibers is specially striking in reptiles and in birds, but also in mammals, where the vagus looses practically all its taste fibers, so numerous in fishes. On the other hand, with the extension of the viscera (lungs and intestine) the general viscero-sensory fibers increase, and consequently the *fasciculus solitarius*, which amongst others contains general fibers from the respiratory tract, increases.

Still more striking, are the changes exhibited by the motor nuclei of these nerves (KAPPERS, BLACK, VERMEULEN).

These changes are due to the different functions of their muscles in the higher vertebrates, and to a different central innervation of the nuclei themselves.

The mammalian facial, glossopharyngeal, vagal and hypoglossal cells show great topographical changes compared with those of the lower vertebrates.

[1]) Cf. HORNE CRAIGIE. Introduction to the finer anatomy of the central nervous system based upon that of the Albino rat. Toronto and Philadelphia 1925.

[2]) The change in the site of the nucleus has resulted in calling the cochlear root of the VIII nerve in mammals, the ventral octavus root, while in reptiles and birds it is called the dorsal octavus root.

[3]) This author found the olive to send fibers in the lateral lemniscus, as well as in the fasc. longitudinalis medialis.

The difference in the *motor facial nucleus* is especially instructive. Being a motor gill nucleus in Plagiostomes and Teleosts its place is determined by the sensory gill centers and gustatory tracts (cf. p. 121).

In frogs (fig. 91 A) where these tracts disappear, the nucleus keeps the primitive position, behind the dorsal trigeminus nucleus (RÖTHIG, BLACK). In reptiles, with the onset of terrestrial life, the corresponding sensory root, specially its gustatory component, becomes of still less importance. The motor VII nucleus, in these animals leaves its dorsal place and shifts somewhat ventrally together with glosso-pharyngeus cells. Though its proprioceptive fibers remain in the sensory VII root (DAVIS, GERARD), with the atrophy of its cutaneous components the motor facial nucleus comes under the influence of the sensory trigeminus, especially in mammals, where the facial musculature [1]) extends over the head, acquiring reflectory connections with the sensory trigeminus (mouth, nose), the eye, and ear. As a consequence of this the motor VII nucleus shifts ventro-laterally to the region of the descending trigeminus root, and to the bulbar reflectory center of the acoustic nerve, the superior olive, which also has a ventral position, and whose cells influence the ear muscles of the VII.

Moreover, ventral tecto-bulbar fibers, spino-mesencephalic collaterals [2]) and cortico-fugal pyramidal fibers enter the nucleus. The combined action of all these ventral impulses in mammals causes its cells to acquire a totally ventral position. Only its para-sympathetic, praeganglionic cells, whose neurites go to the spheno-palatine ganglion (for lacrymal secretion), and to the ganglion of the sublingual and submaxillary salivary glands, retain a more dorsal position, the former in front (see fig. 91 D) and the latter more caudally near the praeganglionic salivary cells of the glossopharyngeus (YAGITA and HAYAMA), whose neurites synaps in the otic ganglion (parotis secretion, cf. fig. 47).

Evidently both salivary cell groups remain under the influence of the center of taste and general visceral sensation (G. C. HUBER), that keep a dorsal location in the oblongata.

---

[1]) For the development of the facial muscles in mammals I refer to ERNST HUBER's papers. Anat. Anzeiger, Bnd. 51, 58, 59, 61 and the Journ. of Comp. Neur. Vol. 42, 1927.

[2]) These are collaterals of EDINGERS secondary protopathic tract conducting pain impulses. Think of the "faces" we make when feeling pain.
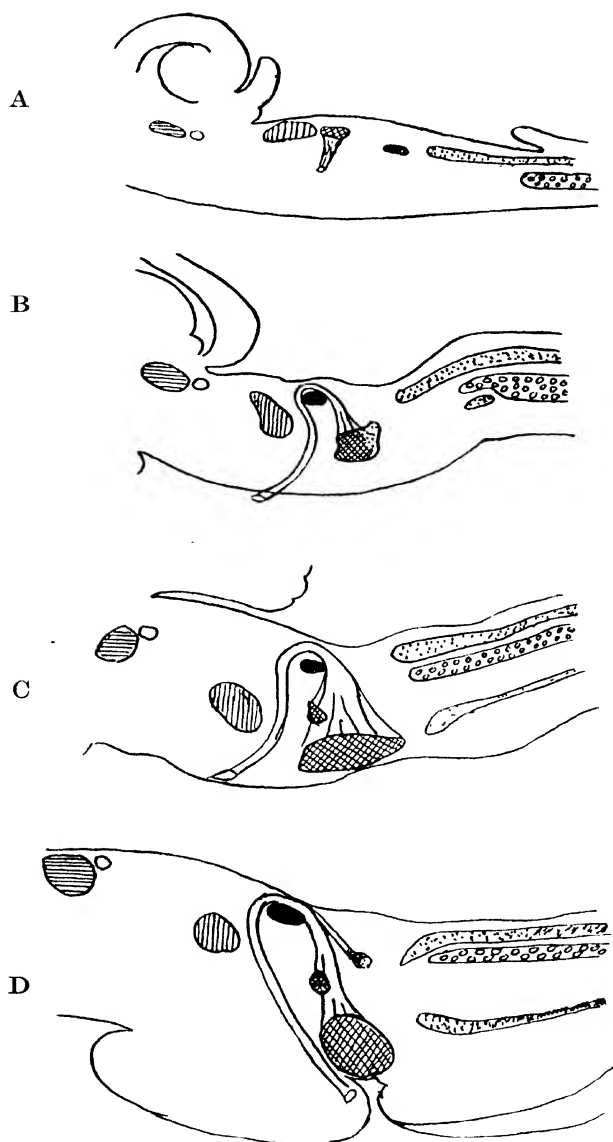
Fig. 91. The position of the motor oblongata nuclei
in the frog (A), lizard (B), hedgehog (C) and man (D).
For explanation of the markings, see fig. 67, p. 122.

Equally striking are the changes observed in the motor *glosso-pharyngeus* and in some of the *vagus cells*, all of which, in fishes and Amphibia, lie in the dorsal region of the oblongata, but some of which, in reptiles [1]) and in birds, start to migrate ventro-laterally.

In mammals, all motor *glossopharyngeus* cells (except those of the parotis salivary nucleus) have acquired a ventral position behind the ventral VII nucleus, forming the frontal part of the "nucleus ambiguus", thus named because its caudal part consists of vagus cells.

The motor *vagus* nuclei of the lung and intestines maintain a dorsal position, near the viscero-sensory center of the lungs [2]) and intestines. According to F. H. LEWY's researches (l. c.) this nucleus also includes important metabolic centers. At the calamus the dorsal vagus nucleus may cross the midline (nucl. motor. comm. vagi; VERMEULEN) as some fibers of the fasc. solitarius do (comm. infima).

The ventral motor cells of the vagus, together with the ventral glossopharyngeus cells forming the *nucl. ambiguus*, innervate striated muscles connected with the larynx.

Apparently the migration of these ventral IX—X cells, is due to impulses proceeding from ventral tracts that influence these nuclei. We do, however, not yet know the character of these impulses. Perhaps they are collaterals of the spino-mesencephalic tract.

According to KOSAKA, the inhibitor nucleus of the heart, though parasympathetic, is also included in the ventral vagus nucleus.

A peculiar feature of mammals is the development of the *spinal accessory*, which, in sharks, starts as a single root, emerging behind the motor vagus roots, but which in mammals extends far backward into the spinal cord, in man unto the fifth cervical segment, being enlarged by local additions in the cord (cf. BECCARI and VERMEULEN).

The *hypoglossus*, innervating the tongue muscles, is derived from

---

[1]) Why the ventral IX cells are connected with the ventral VII nucleus in reptiles (see Fig. 91 B) and with the ventral X nucleus in mammals (Fig. 91, C and D), I do not know.

[2]) In the motor center connected with breathing, a rather large capillary bloodvessel has often struck me in some mammals in connection with HERING-BREUER's theory of respiration, which involves that the carbondioxyde of the blood stimulates this nucleus. Perhaps this special vascularization may have to do with a chemical stimulation of the respiration centre.

ventral spino-occipital roots in Plagiostomes, that innervate the oral portion of the ventral musculature of the trunk. In amphibia, reptiles, birds and mammals, with the outgrowth of tongue muscles from this musculature, the XII nucleus becomes gradually independent.

Since the tongue together with the palate is the chief bearer of taste buds in mammals, the taste center, together with the tactile V, VII and IX fibers of the tongue influences the position of its nucleus.

The change in the reflectory innervation of this musculature is — in a way — analogous to the change in the reflectory inner-vation of the motor VII nucleus, as also in the case of the hypo-glossus its own sensory roots atrophy [1]), as does the sensory root of the facialis, that originally dominates the function of the whole motor VII nucleus. As the motor VII nucleus comes under other impulses, so the hypoglossus nucleus comes under the influence of tactile V, and tactile and gustatory VII and IX fibers of the tongue.

As the chief sensory reflex fibers of the tongue, the rami linguales of V, VII and IX, all run dorsally in the oblongata (the r. lingualis V, nearly joins the fasc. solitarius in man, cf. WALLENBERG), and come from more frontal regions, so the hypoglossus nucleus acquires a more dorsal, but especially a more frontal position in mammals.

The frontal migration of the XII nucleus is very striking, if we compare its position in mammals to that in Amphibia (fig. 91 A, D).

Also the *eye muscle nuclei* show important changes in Amniota. The dorsal abducens nucleus gradually migrates frontally in rep-tiles, birds and mammals, approaching the Deiters nucleus. In ad-dition a ventro-lateral accessory VI nucleus appears for the nicti-tating membrane and retractor bulbi, determined neurobiotactically by the descending V stimulations (TERNI). In the oculomotor nucleus with binocular vision Perlia's central nucleus for convergency develops, while the praeganglionic EDINGER-WESTPHAL nuclei for the inner eye muscles acquire a strong development in Reptiles, Birds and Mammals (KAPPERS, BROUWER).

---

[1]) A sensory ganglion of the hypoglossus is constant only in embryos (FRORIEP) but may persist in the adult, especially in Ungulates (MAYER 1833). TOUSSAINT found it constantly in the donkey, where VERMEULEN also saw it, and in the mule and sheep. It is less constant in the horse. WILSON and VERMEULEN observed it in the calf and VULPIAN in pigs and cats and dogs.

Further differentiation of the spinal cord.

The changes in the sensory roots and posterior funiculi of the cord, arising with the increase of stereognostic sense, studied so carefully by Brouwer, have been mentioned above (see page 155   157).

The development of the central motor systems in the spinal cord is also interesting because with the development of the motor cortex, cortico-spinal fibers or *spinal pyramidal tracts*, arise, as a spinal analogue of the cortico-bulbar innervation.

These fibers are still few in Aplacentalia and Ungulates, where they only reach the cervical region (King). They increase in number in Rodents, Carnivora and Primates, where they extend through nearly the whole length of the cord, reaching the lower sacral region in man. Forming only 7% of the transverse section of the cord in the dog, they cover 20% of it in a monkey (Cebus) and 30% in man (Bregmann) a progression analogous to that of the stereognostic sensory increase in the posterior funiculi, found by Brouwer.

Two divisions are distinguished, the ventral, and the dorso-lateral pyramids.

The *ventral pyramids* run near the edge of the anterior fissure. In man [1]) they reach the lumbar region (Erb, Kooy), crossing on different levels of the cord. In the porpoise they are the only pyramidal tract (Gans), and poorly myelinated. They influence the trunk musculature, the motor nucleus of which (very large in the porpoise, Hepburn and Waterston) is located in the ventro-medial part of the anterior horn, near the fasc. longitudinalis.

The motor cells of the trunk muscles have already this ventro-medial location in lower vertebrates, in which no pyramidal tracts occur. Their topography is apparently determined by reflectory tracts arising in the oblongata and running in and near the fasciculus longitudinalis, which, in the cord, is situated medio-ventrally.

Probably the same factors that cause the motor cells of the trunk to lie in this position also determine the ventral localization of the ventral pyramids.

I have often emphasized [2]) that in most cases descending tracts do not end in motor nuclei, but nearly always in coordinative centers,

---

[1]) Also in the canadian porcupine (Simpson and King).

[2]) First in the Folia Neurobiologica, Bnd. 1, 1908, p. 511.

and that, consequently, not the motor root cells but centers of coordination determine the final course and ending of such tracts.

Even the position of the motor root cells themselves is determined by centers of coordination, that form the junction of which they are the common outlet (common path: SHERRINGTON).

Consequently the expression "motor" tract must be understood cum grano salis, since the course of descending tracts, as that of other tracts, is primarily determined by correlated stimulations.

Very instructive in this respect is the fasc. uncinatus which arises in the cerebellum (p. 165) and ends in a region where motor root cells do not occur at all, but cells that receive vestibular impulses. Apparently cerebellar and vestibular functions are often correlated being simultaneously stimulated by positional changes of the body.

The same principle is demonstrated by the fact that the descending cortical tract, arising in the hippocampus, the fornix (which may be considered a hippocampal pyramid) does not end in a motor nucleus, but in the hypothalamus, that is already correlated with olfaction before the fornix appeared. The same occurs with the fibers arising in the area striata and ending in the lateral geniculate body and corpora quadrigemina anteriora (cf. p. 155). Also the pyramidal fibers influencing eye movements do not end in the eye muscle nuclei [1] but in a regions already related with vision and eye nuclei both, before the "oculomotor" pyramids appeared. Neurobiotactic studies show that a new axonic system generally grows out to a center, the stimulation (or formation) of which just precedes that of its own center of origin.

So, however great the inducement may be to say that the course of the ventral pyramid is determined by the ventro-medial location of the trunk nuclei, it is more probable that the location of both is determined by reflectory tracts preceding the formation of the pyramids.

This conclusion, is strikingly illustrated by the fact that the *dorsolateral pyramid* does not originally descend in the lateral, but in the dorsal funiculi, which are prevailing sensory, and the formation of which preceeds the formation of the pyramids.

This course is seen in Marsupials (ZIEHEN), Ungulates (SIMPSON) and Rodents (fig. 92 A), where the *dorsal* pyramid runs as far down as the lumbar region, and where no termination in motor cells ever could be observed (REVELEY).

---

[1] C.f. also WALLENBERG. Arch. f. Psychiatrie. Bnd. 76, Heft 1, 1925, p. 46.
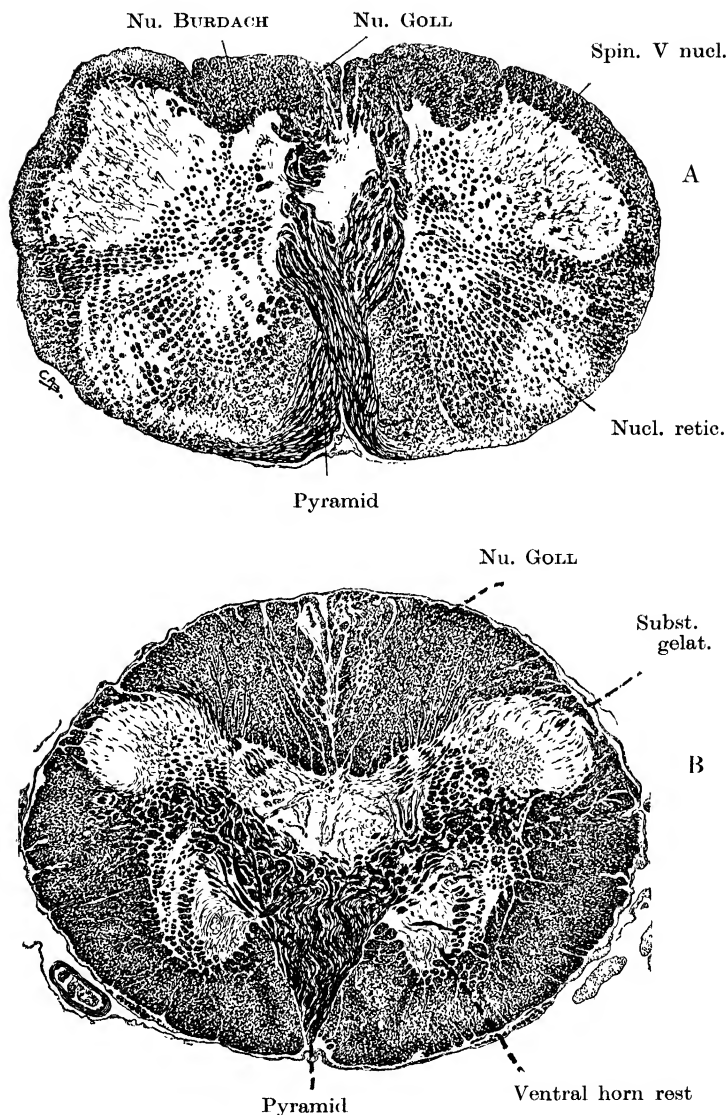
Fig. 92.
Course of the pyramidal fibers after their decussation to the posterior
funiculi in a rodent, Arctomys (A), and to the dorso-lateral funiculi in
a monkey, Cebus (B).

In Carnivora and Primates (fig. 92 B), they run in the lateral funiculi, near the posterior sensory horns and do not acquire direct relations with the motor cells themselves.

Still the influence of the cortical pyramids on the regulation of movements is beyond doubt.

Whereas, in lower vertebrates as birds and reptiles, the position of the body and limbs is regulated by descending midbrain and
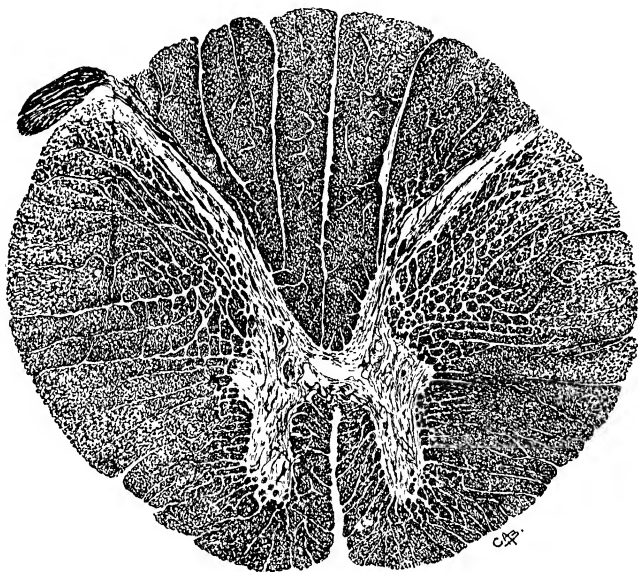
Fig. 93. Second cervical segment of the human cord.
Note the large size of the posterior funiculi, compared to those in the shark, fig. 57.

oblongata tracts, chiefly the tr. rubro- and vestibulo-spinalis which, in mammals, still have the greatest influence on positional reflexes (MAGNUS [1]), DE KLEYN, RADEMAKER, MUSSEN), the pyramidal tracts inaugurate a new regulation of motility, only occurring in mammals and attaining its highest degree in man.

But this influence is more a regulating, even in a certain way, an inhibiting [2] one.

---

[1] MAGNUS Körperstellung, Springer, Berlin, 1924.

[2] After their destruction, the muscle reflexes are higher.

So much is sure that the lateral pyramidal tract which in primates and man runs dorsal to the motor centers of the arms (legs) and fingers (toes), cannot be said to determine the place of these centers. Here again the place of the motor nuclei is apparently defined by reflectory tracts and correlations already existing in a primitive
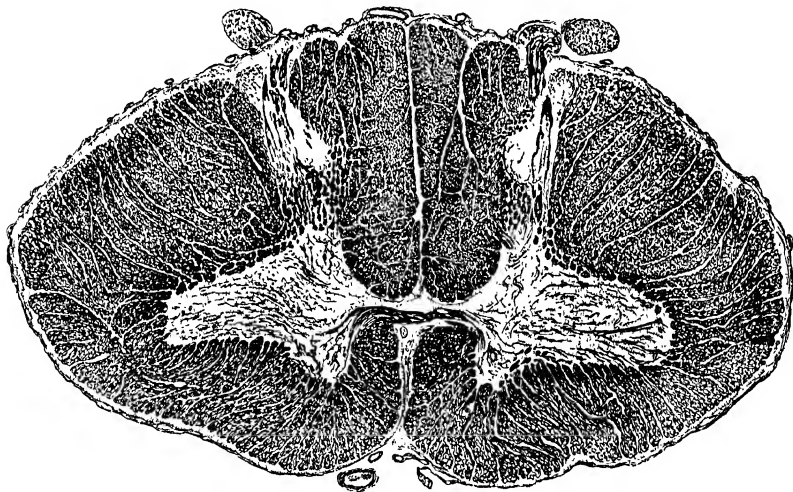
Fig. 94 A. Section through the cervical enlargement of a normal man.
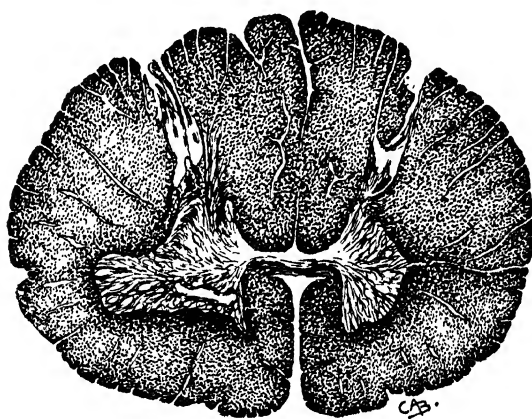
Fig. 94 B. Section of the cervical enlargement of a man
in a case of arm amputation.

way in animals that have no pyramids. For the centers of the extremities this may be the *rubro-spinal tract*, the exquisite reflectory path of positional reflexes that already occurs in reptiles and birds, and that also runs in the lateral funiculi.

Whereas on those levels of the spinal cord that innervate only trunk musculature, practically the same arrangement of the ventral horns (fig. 93) occurs as in fishes, in the cervical and lumbar enlargements, large dorso-lateral cellgroups are added (cf. fig. 94 A and B).

The differentiation of the cellgroups innervating the fingers, is specially striking in man, even in comparison to the anthropoids.

Extensive studies are made on the localizations of the nuclei innervating the different muscles (BRUCE, DEJERINE, SANO, KAISER, WINKLER, SERGI a. o.).

Although the arrangement of the different cell groups in the spinal cord is not so easily explained as the topography of the oblongata (and midbrain) nuclei, KRAUS and WEIL rightly suppose neuro-biotactic factors to be the chief causative agent of motor localizations also in the spinal cord.

As mentioned above, the arrangement of the cells supplying the trunk muscles may probably be explained by their relationship to the vestibular reflexes in the fasciculus longitudinalis, and the dorso-lateral localization of the cells for the hands and feet, by their correlation with positional rubro-spinal reflexes.

The *praeganglionic sympathetic centers*, especially developed in the thoraco-lumbar region, are located in the intermedio-lateral horn (GASKELL, ONUFF, COLLINS, TAKAHASHI, JACOBSOHN, BOK [1])), near BOK's *tr. intermedio-longitudinalis*, a sympathetic reflex path, running near the latero-ventral edge of the substantia gelatinosa, in which sensory sympathetic fibers end (RANSON, BOK).

This location is similar to the one observed in the bulbar prae-ganglionic centers, that also retain their position near sympathetic reflex centers, on the level of the *sulcus limitans*, which, however, is obliterated in the adult spinal cord.

The anterior roots of the cord contain all the praeganglionic fibers which no more run in the dorsal roots as part of them does

---

[1]) See specially BOK: Das Rückenmark, in Möllendorff's Handbuch der mikrosk. Anatomie, Springer, Berlin 1928.

in fishes and Amphibia (HAZAMA [1]). Among these are also fibers whose post-ganglionic neurones go to the striated muscles, subserving their autonomic innervation. The autonomic character of these *accessory fibers* (BOEKE, AGDUHR, TERNI, KUNTZ) has been recently questioned (HINSEY), but there is much to be said in favor of it (cf. p. 86), although their exact function is by no means settled.

S. DE BOER and J. HUNTER asserted that the accessory fibers have an influence on muscle tonus. Though neither AGDUHR nor BOEKE were able to see any alteration in the ordinary tonus of the leg after the extirpation of its postganglionic neurones, and BRÜCKE, BARENNE, RANSON and HINSEY also doubt this, it is sure that cutting of their fibers that end in the sarcoplasm of the muscles (BOEKE, KUNTZ), gives rise to an earlier onset of fatigue (NAKANISHI [2]; see also ORBELI [3]) and GINEZINSKY). Apparently these fibers influence the sarcoplasmatic auto-tonus of the muscles that on the long run again may influence BRONDGEESTS reflectory (fibrillar) tonus (cf. also BELLONI [4])).

Whether there are sensory proprioceptive fibers in the anterior spinal roots as occur in the abducens, trochlear and oculomotor nerves (TOZER and SHERRINGTON), and probably in the hypoglossus, is doubtful.

[1] BUNITI HAZAMA. Untersuchungen über die vasomotorischen Nerven in Radix anterior und posterior des Rückenmarks von Bufo bufo (Japanese), quoted after National Research council of Japan I Anatomy, Transactions and Abstracts, Vol. 1, No. 3, Tokyo, 1928, p. 66.

[2] M. NAKANISHI. (Physiol. Institut d. kaiserl. Univ. Keyo): Eine einfache Methode z. Bestimmung der Reizschwelle für die sympathischen Skelettmuskelnerven; Grütznersche innere Unterstützung. Journ. of Biophysics, Vol. 2, 1927, p. 81. The same: Über den Einfluss des sympathischen Nervensystems auf Skelettmuskeln 1, ibidem; 2. Die Wirkung der successiven Reizung des Sympathicus auf den tätigen Muskel. Acta Medicinalia (Keyo) Vol. 11, Mai 1928, Heft 2.

[3] BRÜCKE, Orbelis Untersuchungen über die sympathische Innervation nicht vegetativer Organe, Klinische Wochenschr. 1927, I, p. 703—704.

[4] BELLONI, Studi sol tono dei muscoli striati. Rivista di patologia nervosa e mentale, vol. 29, 1924.

METABOLIC TISSUE OF THE CENTRAL NERVOUS SYSTEM.

While the specific function of the nervous system depends upon its nervecells and their connections with the periphery, its *metabolism* largely depends upon the *non nervous tissue,* surrounding these elements and the entire nervous system.

The study of this tissue has much increased in importance since
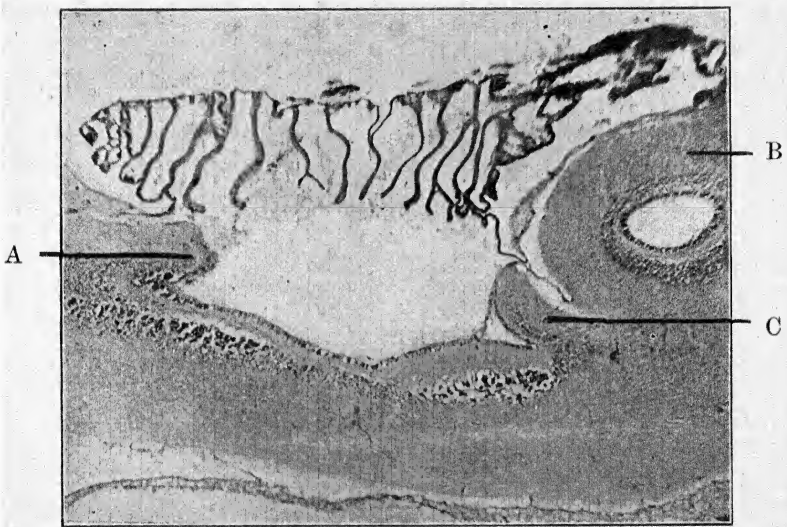
Fig. 95. Choroid of the fourth ventricle of Petromyzon; A, calamus; B, tectum mesencephali; C, cerebellum. The ventricular space under the choroid roof is very wide.

we know that its functions greatly influence the normal action of the neurones and also act a large part in the pathology of the nervous system.

It is sometimes difficult to be certain about its origin, as it is not always easy, or even possible, to distinguish exactly ectodermal derivatives from the mesodermal ones, even in vertebrates. (cf. p. 188).

In invertebrates, where ventricles do not occur internal ependyma and choroid membranes fail, but in Arthropods an external lining

epithelium of ectodermal origin may occur (CAJAL and SANCHEZ [1]) with long offshoots entering the brain: a sort of ependyma externa.

With *Worms, Arthropods Molluscs* real glia cells occur round the ganglion cells and the fibers in the central organs. In Molluscs they even form trophospongial nets (see p. 188) in those cells (JAKUBSKI [2]).
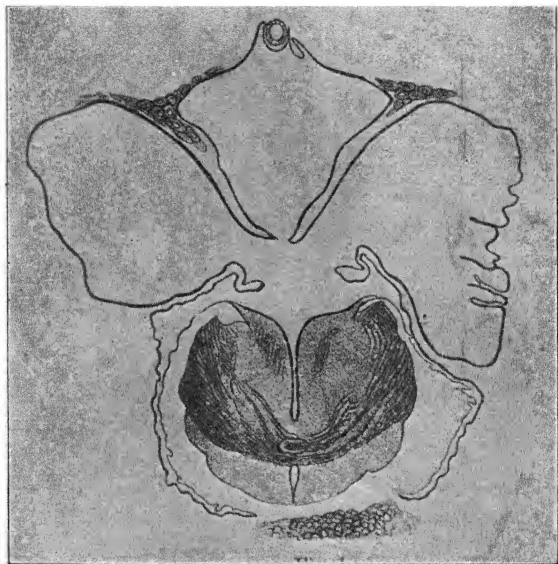
Fig. 96. Cross section through the frontal part of the thalamus of Lepidosteus showing the large dorsal, lateral and ventral sacs of the third ventricle.

In vertebrates, which differ from invertebrates by having a hollow nervous system, the non nervous ectodermal elements, which play a part in the metabolism of the central nervous system, are distinguished in three groups: the *choroid*, the *ependyma* and the *glia*.

The *choroid* forms the ventricular plexuses, which, in mammals, are relatively larger in fetal life (LOEPER) than in adults. Conform herewith is that they never attain such a large relative size in

[1] Cf. HANSTRÖM, Vergleichende Anatomie des Nervensystems der wirbellosen Tiere. Springer, Berlin, 1928.

[2] Untersuchungen über das Gliagewebe der Mollusken Zeitschr. f. wiss. Zool., Bnd 104 and 112.

higher animals as they do in some lower fishes (fig. 95 and 96).

The choroid membranes consist of a layer of cubical or cylindrical cells, between which a homogeneous substance occurs, as is best observed in tangential sections.

The cells, especially in embryonic or young stages, are provided with active cilia (STUDNIǪKA, STERN, KRAMER, BROOKOVER a. o.). In older individuals these cilia often disappear.

The side of the cell turned towards the ventricle is frequently hyaline, and somewhat striated, probably a result of its secretory function. This function also appears from the fact that the cells are often covered with a layer of precipitated albumen.

The protoplasm of the cells exhibits fine granulations that first appear round the nucleus, arising partly from it, and in the protoplasm are enlarged by an additional substance (GALEOTTI).

These basophile granulations or *globuloblasts* (SCHÖPFER) are said to be provided with a thin lipoid membrane. Besides, acidophile granulations occur (GOLDMANN), and oxydases (PIGHINI).

The choroid epithelium is strongly vascularized, its blood vessels being large capillaries provided only with endothelial walls, that may lie immediately against the epithelium of the *choroidal villi*.

These *villi* are considered as glands, secreting substances into the ventricle. On the other hand, the ventricular liquor may pass through the choroid into the meninges.

In the meningeal tissue, above the choroid villi, sometimes also on their ventricular side (KOLMER [1]), large mononuclear cells may occur, a kind of "mast" cells (SUNDWALL), which GOLDMANN called *pyrrol* cells, since they stain deeply with pyrrol blue.

DEWEY supposes them to be of lymph endothelial origin. Their granules, according to my experience, also stain deeply with WEIGERT's lecithine stain.

These granule cells are very numerous in lower animals. In Lepidosteus ASA CHANDLER found them to form a massive structure near the calamus scriptorius. VAN DER HORST called this mass of granular cells, among which also dark pigmented cells occur, the *myelencephalic gland* [2]. He observed it in all Ganoid fishes (cf. also TILNEY).

---

[1] KOLMER. Ueber eine eigenartige Beziehung von Wanderzellen zu dem Choroidplexus des Gehirns der Wirbeltiere. An. Anzeiger, Bnd. 54, 1921.

[2] VAN DER HORST. The myelencephalic gland of Polyodon, Acipenser and Amia. Proc. Kon. Akad. v. Wet. Amsterdam, 1925.

It seems as if this *glandula myelencephalica* has to do with the metabolism of the blood circulating in the choroid, the more so as it is well provided with blood vessels.

The choroid itself plays an important part in protecting the nervous system, as it prevents several substances that may occur in the blood to enter the ventricles as e. g. bile pigments. Among the substances for which it is a barrier are, however, also some antitoxines (as that of the tetanus and diphteria), and some medicinal substances (MEYER and RANSON).

In its selective function the choroid exhibits some similarity to the placenta (hence: "placenta cerebralis").

Further the choroid has an influence on the regulation of the osmotic and ordinary liquor pressure.

The gland like character of the choroid is proved also by drugs which influence its function by means of the autonomic system.

That the choroid membranes so often bulge outward in fishes (cf. fig. 95 and 96) and fetus, is due to the fact that the ventricular fluid develops earlier, phylogenetically and ontogenetically, than their outlet in the arachnoidal spaces (p. 195). This involves, that the accumulation of fluid in the ventricle preceeds the drainage of this fluid through the choroid into the meninges.

As soon as the draining function of the choroid increases its villi extend further into the ventricles.

The choroid of the fourth ventricle in mammals is pierced by the lateral foramina of LUSCHKA (STRONG [1]), GREENE, OLIVEIRA, RASMUSSEN [2])). The foramen of MAGENDIE does not exist normally in lower vertebrates (KAPPERS) and in man (v. MONAKOW, HUBER, KAPPERS). In man it may be made by lifting up the cerebellum.

The choroid continues in the *ependyma*, which forms the lining of the cavities of the brain and of the central canal of the cord (fig. 97). The ependyma has a metabolic, and supporting function.

The ependyma cells are generally cubical, but on certain spots, e. g. below the commissura posterior of the midbrain, and above the comm. anterior of the cord, they may be much higher.

Their ventricular side is also provided with cilia, occurring either in tufts or solitary. These cilia move (VALENTIN, PURKINJE, PUTNAM).

---

[1]) STRONG, GREENE and OLIVEIRA. The lateral aperture of the fourth ventricle in man. Anat. Record, Vol. 32, 1926, p. 223.

[2]) Additional evidence favoring the normal existence of the lateral apertures of the fourth ventricle in man. Anat. Record, Vol. 33, 1927, p. 179.

The ependymal cells differ from the choroid cells by a very long peripheral offshoot, that originally runs radially through the entire thickness of the nervous system, ending in trumpet-like feet, that join to make the external limiting membrane (fig. 97, at the right).

This is permanent in lower animals, even in adults. In the higher
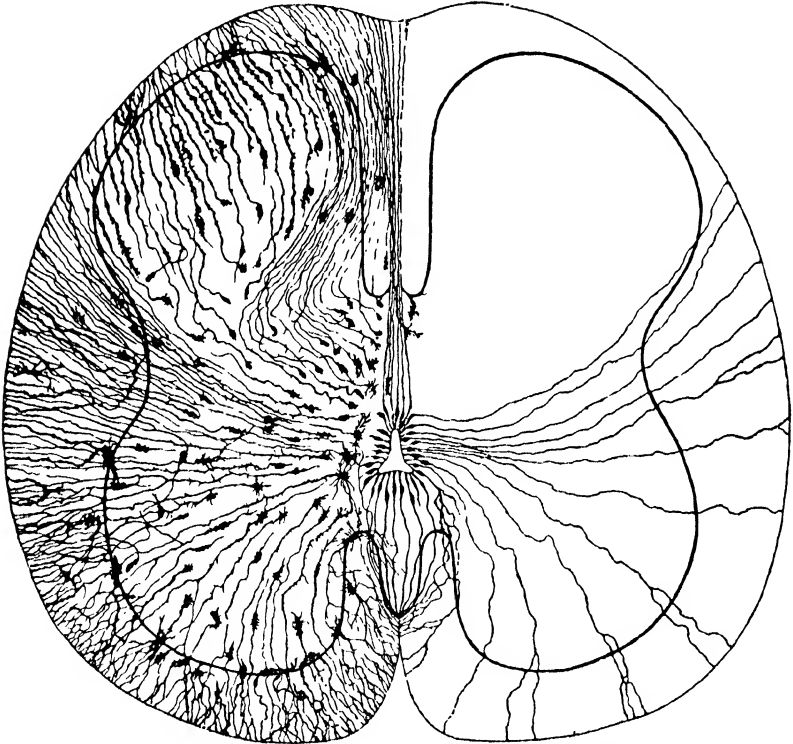
Fig. 97. Ependyma cells (right) and different stages of glioblasts (left) in the spinal cord of a 14 c.M. human fetus, after v. LENHOSSEK.

it is most evident in fetuses. The peripheral offshoots probably take up oxygen or at least anabolic substances for the ependyma cell.

This is made probable by the fact that in animals which have no intra-spinal blood vessels also the dendrites of the ganglion cells extend unto the periphery (Ammocoetes, TRETJAKOFF, and fetuses of higher animals). As these dendrites contain oxydases they apparently take up oxygen from the periphery.

In adult mammals, not all the ependyma fibers extend as far as the periphery, the limiting membrane being largely made by similar end feet of glia cells.

Another metabolic function of ependyma cells is undoubtedly shown by the peculiar glandular structures, in the thalamus of fishes, reptiles, birds and mammals (KAPPERS, CHARLTON [1]) whose rich vascularization and albuminous surface covering clearly point to a secretory function (fig. 98). In Polyodon this structure even extends into the
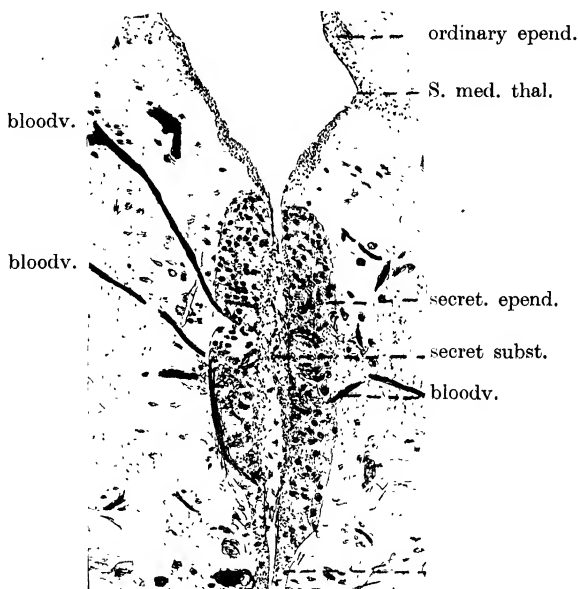
Fig. 98. Richly vascularized secretory ependyma in the thalamus of a fish (Monopterus).

forebrain (HOCKE HOOGENBOOM [2]). Near it runs N. HOLMGRENS *tr. griseo-tuberis*, fibers of which perhaps innervate this gland (CHARLTON). In birds and mammals it is less developed than in lower vertebrates, and hitherto I failed to find it man.

In mammals, however, WISLOCKI and PUTNAM showed that in the area postrema dye stuffs may penetrate from the bloodvessels into the ventricle, and, vice versa, through the ependyma in the blood.

---

[1]) CHARLTON. A gland-like ependymal structure in the brain. Proc. of the Kon. Akad. van Wetensch. Amsterdam, 1928.

[2]) De hersenen von Polyodon folium, Lacep. Dissertation, Amsterdam, 1928.

In connection with the transmission of particles from the ventricle through the ependyma, it is interesting that FREDERIKSE found a similar intercellular substance between ependyma cells as occurs between choroid cells.

In this respect the ependyma thus exhibits a close relationship with the choroid. Besides, fatty granules can be pointed out therein, particularly in young animals.

Only a part of the original embryonic lining cells of the cavities develops into ependymal cells, retaining their position on the surface of the ventricles and keeping their cilia.

Another part are *spongioblasts*, which, originally also provided with cilia, loose them, changing their form, position and function.

Their cell bodies come to lie at some distance from the surface, keeping contact with it only by means of a protoplasmatic offshoot, that — in contrast with the deep offshoot —, may be called the central offshoot.

These *bipolar spongioblasts*, by mitotic division, give rise to more bipolar spongioblasts (DE CASTRO).

The central offshoot then atrophies and *unipolar spongioblasts* result (fig. 97), the offshoot of which grows deeper into the nervous system.

The centrosome, originally located towards the central canal, then lies opposite the deep offshoot (DE CASTRO).

These bipolar and deep unipolar spongioblasts are *glioblasts*.

Apart from such glioblasts, that arise from spongioblasts, there is still another source of glia cells, not arising from cells that are from the beginning predestined to form glia, but from cells that have remained on a lower, neutral stage of development, so that they may be called only *medulloblasts*, as they may form neuroblasts as well as spongioblasts.

Also these medulloblasts do not remain in the wall of the central canal, but may shift in the depth of the nervous system (HIS, SCHAPER).

They may even keep their indifferent form in the adult and not rarely give rise to tumor formation, as, however, also the other glia may do, with the exception of the microglia (see below; BAILEY and CUSHING).

They may also, however, develop further, either into neuroblasts or into spongioblasts.

Hence results that spongioblastic development is not restricted to

the lining epithelium of the medullary tube, but also occurs inside the nervous system from bipolar glioblasts and medulloblasts.

The spongioblasts developing from the latter mostly start as unipolar forms.

The unipolar spongioblasts, from whatever origin, undergo a further transformation. Their deep offshoot grows out in the direction of capillaries or of the outer surface of the nervous system forming with their trumpet-like endings or sucker feet, the membrana limitans perivascularis and superficialis (fig. 99 A and B).

At the same time, smaller offshoots arise in all directions from the cell body and may surround the neurones.

They are then called *astroblasts*. In some of these astroblasts gliafibrillae develop, in others not.

The former are called *fibrillar*, the latter *protoplasmatic astrocytes*, both, however, may be in contact with blood vessels, with ganglion cells, or with the surface.

Specially amongst *protoplasmatic glia-cells* giant forms occur, having large, more or less oval nuclei with little chromatine. One special form of protoplasmatic glia is the *oligodendroglia*, being only provided with few offshoots and mostly lying in the white substance, although they may as well occur in the grey substance.

Specially near the margins the glia may form an anastomozing network (HELD). It has, however, not yet been settled whether they form a real syncytium, as supposed by HELD, HARDESTY and FIEANDT (cf. SPIELMEYER's excellent work on this subject [1])).

All glia cells may continue to divide amitotically.

The fact that in the early stage of development (see above) the spongioblasts divide mitotically, and that later the glia divides amitotically, seems to confirm PETER's rule, that specialized tissue divides amitotically, whereas mitoses mainly occur in not yet or less specifically functioning tissue.

A special form of glia is ROBERTSON's and HORTEGA's *microglia* (wrongly called mesoglia), small, mostly oval cells with small dark nuclei and provided with thin offshoots, that may run in all directions, carrying perpendicular spiny excrescences. They are exquisite migratory elements, occurring as satellites near ganglion cells and capillaries on which, however, they never form trumpet-like endfeet

[1]) SPIELMEYER. Arbeiten aus der Deutschen Forschungsanstalt für Psychiatrie in München, Bnd. VI, 1923.
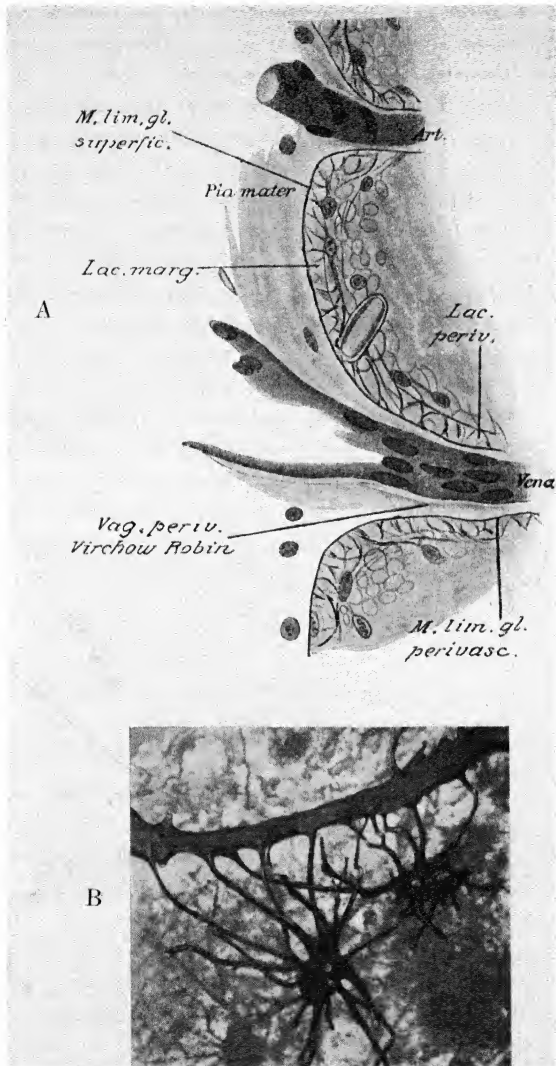
Fig. 99. A. Membrana gliosa limitans superficialis
in the human cortex, after HELD. B. End feet of
glia cells forming the membrana gliosa limitans
perivascularis, after K. H. BOUMAN.

as other glia cells do. They are supposed to be derived, not from
central spongioblasts, but, from the mesenchym surrounding the
nervous system (HORTEGA, PENFIELD, SPATZ).

As this mesenchym (the pia meninx) is of ectodermal origin (arising
from the neural crest, HARVEY, BURR), these cells are also ectodermal.

Some authors, amongst whom PRUYS, believe that these cells are also of
central origin, while BERGMAN [1] who published a very exact study on the
microglia, leaves their origin undecided. I am inclined to believe that they
arise from the pia as they generally first appear periferally.

Finally, *ameboid glia cells* occur, that, according to HORTEGA,
are degenerate glia cells, acquiring a rodlike shape.

They have been especially studied by ALZHEIMER, SPIELMEYER (l.c.)
and JAKOB [2]) and may be numerous in pathological circumstances.

The significance of the central glia for the metabolism of the
nervous system, is evidenced by the fact that the location of these
cells and their branches is apparently determined by blood vessels
and neurones and strongly influenced by inflammations. They may
destroy red blood bodies or ganglion cells (neuronophagie).

Their *trumpet shaped feet* form a membrane round the blood vessels,
the *membrana limitans gliosa vascularis* of HELD, as the marginal
glia forms a *membrana limitans gliosa superficialis* on the surface
of the nervous system. Between the limitans gliosa perivascularis
(which is covered by a pial lining, the membrana intima piae), and
the vessel, a narrow space remains, the space of VIRCHOW-ROBIN,
that peripherally communicates with the arachnoidal spaces of the
meninges and thus forms an outlet into the meninges (fig. 99 A).

Besides, NAGEOTTE, MAWAS and ACHUCARRO have pointed out
that glia cells also possess a secretory function, an inner secretion,
which may influence the general nervous disposition.

Their metabolic function appears from the glycogen found in
them by CASAMAJOR and TERNI and from the *trophocytes* whose
offshoots, entering the intervertebral ganglion cells may be canali-
culized (NEMILEFF), and often contain lipoid substances (*trophos-
pongium*, E. HOLMGREN).

*We thus find in the choroid, ependyma and glia a relationship to the
metabolism of the nervous system. In connection herewith it is interesting*

[1]) De cellen van HORTEGA en hunne kleuring. Dissertation, Utrecht, 1927.
[2]) A. JAKOB. No male und pathologische Anatomie und Histologie des Gross-
hirns. Bnd. I Normale Anatomie und Histologie und allgemeine Pathologie, 1926.

*that the invasion of the nervous substance with glia cells only acquires
a greater significance with those animals that possess intracerebral
blood vessels, and may increase under pathological conditions.*

Amphioxus, in the central nervous system of which no blood vessels
occur, chiefly possesses ependymal cells and fibers in its spinal cord,
and even in the spinal cord of Petromyzon, where intraspinal vessels
are also lacking, similar relations occur. Although the latter has cells,
that are no more connected with the central canal, the endfeet
of these cells still all extend to the limitans superficialis, reaching the
periphery of the cord. Exclusively central glia cells first become
abundant in Plagiostomes, whose cord is richly provided with vessels.

The phylogenetic development of the meninges.

In invertebrates, the term meninges is never applied, although
the sheathlike connective tissue surrounding the ventral cord in Anne-
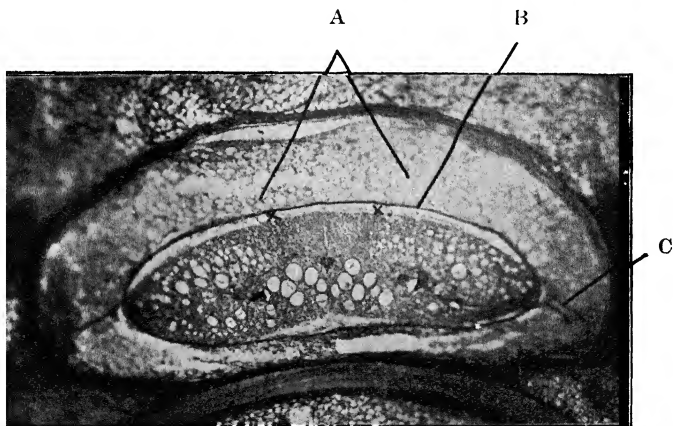
Fig. 100. Spinal cord of Petromyzon in situ; A, perimeningeal
tissue, surrounded externally by the endochondrium of the
vertebra; B, meninx primitiva; separated from the cord by an
artificial space (xx), caused by shrinkage; C, lateral ligament.

lids (page 29) and Arthropods shows some analogy to the simple
arrangement of the primitive meninx in Amphioxus.

In Cyclostomes (fig. 100) and most other fishes, the thin sheath
of connective tissue that lies closely upon the central nervous system,
is again surrounded by a thick mucous or adipose layer serving as a

buffer tissue between the cord and the vertebrae. SAGEMEHL already
pointed out that this buffer tissue does not belong to the meninx
itself, but is a *perimeningeal tissue*, such as in man still occurs in
minor quantities between the dura and the endost of the vertebrae.
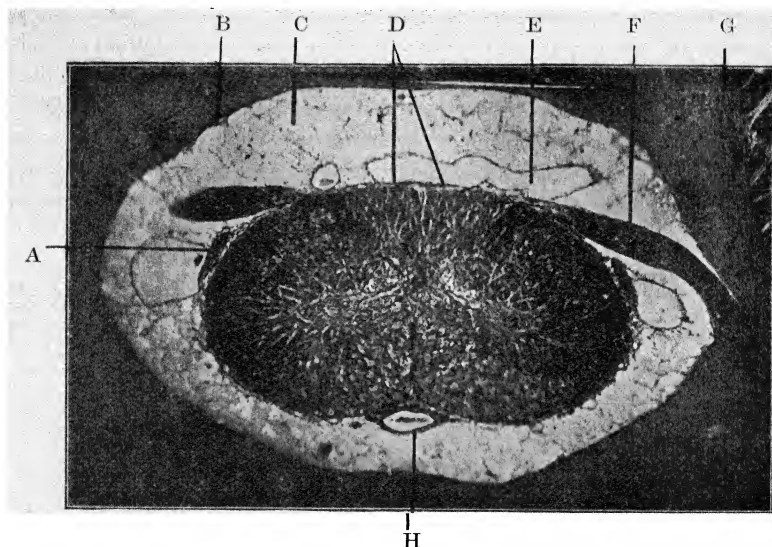
Fig. 101. Spinal cord of Scyllium canicula in situ; A, lateral ligament;
B, endochondrium; C, perimeningeal tissue; D, meninx primitiva;
E, perimeningeal vein; F, radix posterior; G, vertebra; H, arteria
vertebralis anterior.

STERZI [1]) first stated that in Cyclostomes and Plagiostomes only
one meningeal membrane occurs, which he called *meninx primitiva*.

Recently HARVEY and BURR [2]) have shown that the inner part of the
meninx — at least in Amphibia — develops from the neural crest, which
gives rise to an ectodermal mesenchym enveloping the spinal cord, while the
dura and the perimeningeal tissue develop from the mesodermal mesenchym.

[1]) STERZI. Ricerche intorno all'anatomia comparata ed all'ontogenesi delle
meningi. Atti del reale instituto veneto di scienze, lettere ed arti, Anno acca-
demico 1900—1901, Vol. 60, pt. 2, Recherches sur l'anatomie comparée et
l'ontogénèse des meninges. Arch. ital. de biol. 37, 1902.

[2]) HARVEY and BURR. An experimental study on the origin of the meninges
Proceedings of the Society of experimental biology and Medicine, 1924,
Vol. 22.

In Cyclostomes, I could not distinguish different layers in this thin meningeal sheath [1]).

The meninx primitiva of the Lamprey, from which ligaments (fig. 100, E) extend laterally into the perimeningeal tissue, does not yet form septa in the substance of the spinal cord, so that the membrane is easily detached (xx) from the cord during fixation.

The nutrition of the spinal cord is mediated by blood vessels running in this membrane and has to pass through the meninx and through the superficial layer, made by the end feet of the ependymal cells. Intraspinal [2]) vessels do not occur in Petromyzon.

The perimeningeal buffer tissue, surrounding the meninx primitiva, consists of large mucous cells. It reaches as far as the endochondrium of the vertebrae and consequently is considerably developed.

In Selachians, meningeal septa with blood vessels grow into the spinal cord, causing a closer relation between the nervous substance and the vascular system. As, however, the limitans gliosa superficialis everywhere follows those septa, a real

Fig. 102. Spinal cord of Girardinus (cervical) in situ; A, perimeningeal (epidural) sinus; B, vertebra; C, meninx primitiva.

penetration of meningeal tissue and its bloodvessels into the nervous substance itself does not occur, neither here, nor in higher animals.

Also in Scyllium (fig. 101) I found one sheath only (D), in which no differentiation in separate layers is visible.

Here, however, four spinal ligaments (STERZI) occur, the strongly

[1]) The meninges in lower vertebrates compared with those in mammals. Archives of Neurology and Psychiatry. Vol. 15, 1926.

[2]) In the brain of the adult lamprey bloodvessels enter the nervous tissue, accompanied with septa that are again lined by the membrana gliosa perivascularis, so that the bloodvessels nowhere are in direct contact which nervous tissue. This also holds good for higher vertebrates.

developed lateral ligaments (A), and a thin dorsal and stronger ventral ligament. Only the lateral ligament extends for some distance through the perimeningeal tissue. The others are local thickenings of the meninx.

Round this meninx primitiva which, as in Cyclostomes, continues on the root, a large amount of mucous perimeningeal tissue (C) is found in sharks, reaching as far as the endochondrium (B), and showing much more widely spread meshes than in Cyclostomes.

Large perimeningeal veins, consisting only of endothelium without a muscular coat, still failing in Petromyzon, occur in Scyllium, chiefly on the dorsal (E) and on the lateral side of the cord.

The conditions in Ganoids (HOCKE HOOGENBOOM [1])) are similar to those in Selachians, but those in Teleosts vary.

With the small Girardini no differentiation is visible in the thin meningeal sheath surrounding the spinal cord and brain. — There is but little perimeningeal tissue in this animal, the vertebrae lying closely against the cord. Only dorsal to the cord (fig. 102) and round the brain a wide meshed perimeningeal tissue occurs, in which large perimeningeal veins appear.

In *Lophius piscatorius* other conditions obtain. Here the spinal cord is imbedded in a large quantity of fatty wide meshed *perimeningeal tissue*. Moreover, the meningeal sheath itself (fig. 68 and 103) is distinelly differentiated.

The cells lying immediately under the wide meshed perimeningeal mucous tissue form a dense fibrous layer (D.), the beginning of a *dura mater*, which, however, is not yet separated from the leptomeninx (C) by a *continuous* subdural space. As also observed by VAN GELDEREN [2]), in early human embryos (35 mm.), the "ectomeninx" has become a denser tissue, contrasting distinctly with the "leptomeningeal" tissue underneath it without, however, being separated from it over the whole circumference but only by local dehiscences (cf. fig. 68 at the top and fig. 103 at E).

In the leptomeninx, the wide meshed character of its tissue con-

---

[1]) De hersenen van Polyodon folium, Lacép. Dissertation, Amsterdam, 1928.

[2]) VAN GELDEREN. Zur vergleichenden Anatomie der Sinus durae matris, Anat. Anz. 58, 1924.

Compare also VAN GELDEREN. Ueber die Entwicklung der Hirnhaute bei den Teleostiern. Anat. Anzeiger Bnd. 60, 1925- 26.

trasts with its sheathlike character in lower fishes. We may distinguish an exterior leptomeningeal layer, C, from an interior one, B.

In the former, lying directly underneath the dura, the cells stand perpendicular on an external subdural (arachnoidal) membrane. In the interior part, B, the meshes are much less regular. Another difference is, that only the interior layer follows the membrana intima piae in to the septa, and that it contains several arteries,
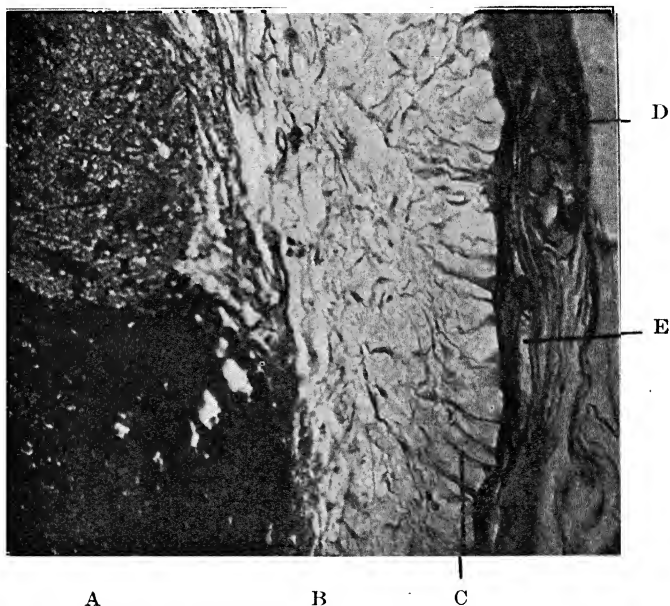
Fig. 103. Enlarged photograph of the meninges in Lophius; A, spinal cord; B, interior layer of the leptomeninx; C, exterior leptomeningeal layer (palissade cells); D, dura meninx; E, local dehiscence between the dura and leptomeninx (cf. fig. 68).

running immediately along the spinal cord and continuing in the septa.

Although the leptomeninx is wide meshed, especially in its outer part C, it is still very different from the trabecular tissue of a real arachnoid, since real "trabecles", that is, fibrillar threads of connective tissue, covered with mesothelial cells, do not occur here.

The pseudo-trabecles are ramifications of single cells and may be compared to the wide meshed reticular tissue of lymph glands. With real arachnoid cavities the meshes are much wider and the trabecles consist of fibrous bundles (KEY and RETZIUS), that are not so numerous (see fig. 104, 105, 106) and covered with mesothelia.

The loose leptomeningeal tissue in Teleosts does not yet perform a function as important as the arachnoid in higher animals as a receptacle of external cerebro-spinal fluid. It here chiefly performs the same function as does the wide meshed reticular connective tissue in the intestines and lymph glands. Still it points to a differentiation immediately preceding arachnoidal development.
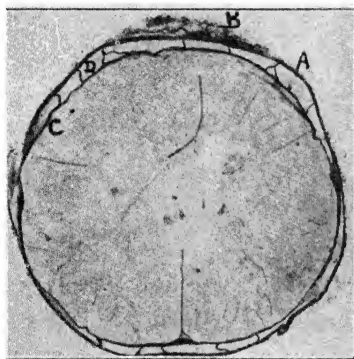
Fig. 104. The well developed dura meninx(A) and arachnoidal space(D) in Athena (owl); B, rest of perimeningeal tissue; C, pia meninx.

Fishes consequently do not have actual arachnoidal cavities, and even the Teleosts have no, or very little *liquor cerebrospinalis externus*, which, in mammals, fills the large subarachnoidal cavities, and the total volume of which, in man, considerably surpasses the volume of the liquor cerebro-spinalis internus or ventricular fluid.

Together with the absence of external cerebro-spinal fluid, we see the striking fact that the quantity of internal cerebro-spinal fluid — ventricular fluid — is not seldom very large in fishes.

The relatively large volume of liquor cerebro-spinalis internus is not only proved by the wide ventricles (specially rhomboidal ventricle) in Cyclostomes and Sharks, but also by the fact that their choroid membrane generally bulges outward. This is shown by the roof of the fourth ventricle in Petromyzon (fig. 95) and Ceratodus, and in Lepidosteus and Amia by the choroid roof of the third ventricle (the parencephalon), which on all sides evaginates to such a degree that choroidal sacs, filled with ventricular fluid, extend far outside along the brainwall, frontally as well as caudally (fig. 96).

The large volume of the ventricles and consequently of the ventricular fluid in these fishes, forms a strong contrast to the

absence of arachnoidal cavities and external cerebrospinal fluid.

In Amphibia the relations are more advanced (see p. 190. HARVEY and·BURR). Here and in Reptilia and birds, real, though small arachnoidal cavities appear, which in mammals, acquire a large size, especially in Primates. In the latter, the choroidal membranes with a single exception [1]), grow deeper into the ventricles as draining organs, while the liquor externus in the arachnoidal cavities increases.

The coincidence of the accumulation of arachnoidal fluid, on one hand, and the growing of the choroid membranes into the ventricles, the forebrain ventricles chiefly. on the other, secreting fluid into, but at the same time *draining* the ventricles, is not accidental. The liquor externus largely originates from the ventricular fluid, which diffuses through the choroidal membranes.

Fig. 105. Cat, neonatus; Spinal cord in situ. A, epimeningeal veins; B, perimeningeal adipose tissue; C, dura; D, ligamentum denticulatum; E, spinal cord.

This origin of liquor ex-ternus is a very important one, although another outlet of fluid occurs in the Virchow-Robin spaces (fig. 99) around the vessels, and so into the arachnoid cavities.

In view of the fact that a large part of the liquor arachnoidalis originates from the diffusion of ventricular fluid through the choroid, it is not strange that the formation of arachnoidal sacs in mammals occurs simultaneously with a greater draining action, and ingrowing of the choroid into the ventricles.

Hence it appears that of both choroidal functions, the secretion of fluid into the ventricle and the draining of ventricular fluid, the former is the first to appear, and so explains the bulging of

---

[1]) The recessus laterales of the oblongata, pierced by the foramina lateralia of LUSCHKA, keep a protruding form, extending over the octavus root.

the choroidal sacs in lower fishes, as well as the absence of proper arachnoidal cavities in these animals. Only in higher animals, mammals, the drainage function of the choroid becomes more evident.

In the embryonic development the same sequence is observed. WEED [1]) found in pig embryos that ventricular fluid occurs in the first stage of ventricular development, while the liquor externus and arachnoidal cavities appear only in an embryo of 14 m.m.

A few words may be added concerning the dura. Whereas, in Lophius, as in mammalian embryos (VAN GELDEREN, l.c.), only local dehiscenses occur between the dural membrane and the underlying leptomeninx, in adult Reptiles, mammals and birds, the dura is separated from the underlying arachnoid by a small but continuous *subdural space*, that is only passed by the lateral or *denticulate ligament* (fig. 105 and 106, C) connecting the pia with the dura at the intervals between the roots.
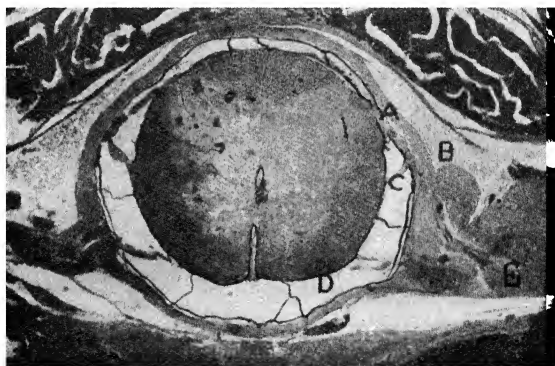
Fig. 106. Cat, neonatus; spinal cord in situ. A, dura; B, perimeningeal adipose tissue; C. ligamentum denticulatum; D, arachnoidal spaces.

This subdural space (visible but not nominated in fig. 105 and 106) in man is only a few m.m. wide. The outer arachnoid membrane which forms its inner limit, allows a slight diffusion inside, but not in outward direction, except at the arachnoidal villi (vide infra).

In the adipose perimeningeal tissue, between the dura and the

---
[1]) WEED, LEWIS. Development of the cerebro-spinal spaces in pig and man. Contributions to Embryology of the Carnegie Institution, No. 5, 1917.

vertebrae, veins occur with thin walls consisting chiefly of endothelium, as in sharks and Teleosts. In the skull they form the large sinuses, the development of which has been so carefully studied by MALL [1], VAN GELDEREN [2] and MARKOWSKI [3]).

The relations in mammals are shown in fig. 105 and 106. It is important to identify the presence of perimeningeal fat (B), lying between the dura and the endost of the vertebrae, and the occurrence of perimeningeal veins in this tissue (fig. 105 A). In fig. 106 it is seen that the dura continues in the epineurium of the roots.

The arachnoidal tissue enters *inside* the roots, as KEY and RETZIUS demonstrated by injections, and as was confirmed by LEWIS WEED [4]), who described small *arachnoidal villi* in the roots, by which the fluid is evacuated into the endoneural lymphspaces of RETZIUS (guaina sussidiaria of RUFFINI).

In the region of the brain, where nerve roots are rare, most of the external cerebro-spinal fluid is evacuated immediately into the blood, by *arachnoidal villi* that lie against the walls of the sinuses. Only a small quantity flows off along the cranial roots, among which the olfactory nerve may act the largest part, enabling the fluid to enter the lymphspaces of the nose.

As a consequence of the large volume of the arachnoid which occupies most of the space in the vertebral canal in higher mammals, the space left for the perimeningeal fat, that serves as a lubricating tissue, is very small. In the skull, which is a much more rigid enclosure than the flexible vertebral canal, the perimeningeal adipose tissue even disappears and the dura, although a separate membrane in the fetus (VAN GELDEREN, l.c.), in adult mammals coalesces with the cranial endost, except where sinuses lie between both.

Where the arachnoidal villi reach these sinuses, the dura is reduced so that the villi are separated only by a thin dural membrane from the wall of the sinuses, in which the cerebro-spinal fluid diffuses.

[1]) MALL. On the development of the bloodvessels of the brain of the human embryo. Am. Journ. of Anat. Vol. 4. 1905.

[2]) VAN GELDEREN. Die Morphologie der Sinus durae matris. Erster, zweiter und dritter Teil. Zeitschr. f. Anat. und Entwicklungsgesch, Bnd. 73, 74, 75, 1924, 1925.

[3]) MARKOWSKI. Entwicklung der Sinus durae matris des Menschen. Bulletin international de l'Académie polonaise des Sciences et des Lettres. Serie B Sciences naturelles IV° supplémentaire, 1921; Cracovie, 1922.

[4]) An Experimental study of the origin of the Meninges, Proc. Soc. Exper. Biol. & Med. 1924, Vol. 22.

DATA FOR AN ANTHROPOLOGY OF THE BRAIN.

Relation Exponents, Cephalization Coefficient.

From the preceding pages it appears that there is a great increase in complexity of the central nervous system, especially of the brain, – a greater cephalization – · in higher animals and in man as compared with the lower forms. This greater cephalization causes the weight of the brain to increase.

It is, however, not the complexity of the brain alone that determines its weight.

Brainweight also depends on the size of the body. The influence of body size on the nervous system appears already in the greater number of root fibers of spinal nerves in larger animals compared with smaller ones. So the number of the motor root fibers increases with the transverse diameter of the total musculature, while the number of sensory root fibers increases with the surfaces of the body and (proprioceptive fibers) with the transverse diameter of the musculature (cf. DONALDSON) [1]), LAPICQUE and GIROUD [2])).

The latter paper is of interest because it shows that, while the relation in the increase of sensory fibers is less than in the motor, the *relation* of the total increase of motor plus sensory fibers in animals of the same species compared to animals of different species but of the same order, is as 0,18 : 0,42 which relation is approximately equal to that of the intraspecial and interspecial relation exponent which is 0,25 : 0,56 (DUBOIS, see also p. 201).

For long endeavours have been made to express in a mathematic formula these two different factors in the brain and body weight

---

[1]) For data concerning the relation between body size and the number and size of peripheral nerve fibers, I refer to DONALDSON's valuable book: ,,The growth of the brain" New York 1895, and to the other publications of this author and his school, especially the nervous system of the American Leopard frog, Rana pipiens as compared with that of the European frogs. R. esculenta and R. temporaria. Journal of comp. Neurol. Vol. 18, 1908 and The Rat 2nd. edition, Memoirs of the Vistar Institute, Philadelphia, 1924.

[2]) LAPICQUE and GIROUD. En fonction de la taille de l'animal le nombre des neurones sensitifs varie moins que celui des neurones moteurs. Co. Rend. de la Société de Biologie, Tome 89, 1923.

relation (BRANDT [1]), MANOUVRIER [2]), MARSHALL [3])). It is evident that the influence of the body weight on the brain weight can be found by comparing animals of the same intellect or cerebral organization, differing merely in size, while the intellectual or cephalization factor can be easier found between animals of the same bodily weight and somatic organization, where consequently the bodily influence on the brain is the same. The question becomes more difficult if the cerebral organization (or cephalization) and body weight both differ.

As it was immediately clear that the influence of body weight is not a simple arithmetic one, BRANDT got the idea that brains of different sized animals of approximately the same intelligence (e. g. cat and tiger) might be related to the surfaces of their body (this being an indicator of their metabolism, which he thought might influence the brain volume). Now the relation of the surfaces of two geomatrically equal bodies is that of the $^2/_3$ or 0,66 potential of their volumes or weights. SNELL [4]) and DUBOIS [5]) accepted the potential relation as a principle, but the latter first realized that it is the peripheral innervation that determines this potential (not the metabolism).

So DUBOIS accepted the formula [6]) $E : e = P^r : p^r$, in which

[1]) BRANDT. Sur le rapport du poids du cerveau à celui du corps chez differents animaux. Bull. de la Société imp. des naturalistes de Moscou, Tome 40, 1867.

[2]) MANOUVRIER. Sur la valeur de la taille et du poids du corps etc. Bull. de la Société d'Anthropologie de Paris, 1882. The same: Sur l'interprétation de la quantité de l'encéphale etc. Ibidem Tome III 1885. Those who have no time to read all the original papers on this subject will find a good exposé in LAPICQUE: Le poids du cerveau et l'intelligence. Journ. de psychologie, année XIX, 1922 and in ANTHONY: Anatomie comparée du cerveau, Doin, Paris, 1928.

[3]) MARSHALL. On the relations between the weight of the brain and its parts and the stature and mass of the body in man. Journ. of Anatomy and Physiology, Vol 26 (N.S. vol. 6) 1893. See also Proc. of the Roy. Soc., London, No. 163, 1875.

[4]) SNELL. Die Abhängigkeit des Hirngewichtes von dem Körpergewicht und den geistigen Fähigkeiten. Archiv. für Psychiatrie, Bnd. 23, 1891.

[5]) DUBOIS. De verhouding van het gewicht der hersenen tot de grootte van het lichaam bij de zoogdieren. Verhandelingen der Kon. Akad. v. Wetenschappen, Amsterdam, deel V, April 1897. See also Bull. de la Soc. d'Anthropologie de Paris, 1897.

[6]) In this formula E and e stand for the brainweights and P and p for the bodyweights.

the potential r is the exponent of brain-body weight relation but he did not a priori accept a value 0.66 for r, but calculated its actual value by the equation $r = \dfrac{\log. E - \log. e}{\log. P - \log. p}$, using the brain and body weight figures collected by M. WEBER [1]). He thus found that r was not 0.66, but, with only slight variations in hundreds of mammals, he found it to be 0.56. The constancy of this figure was striking,
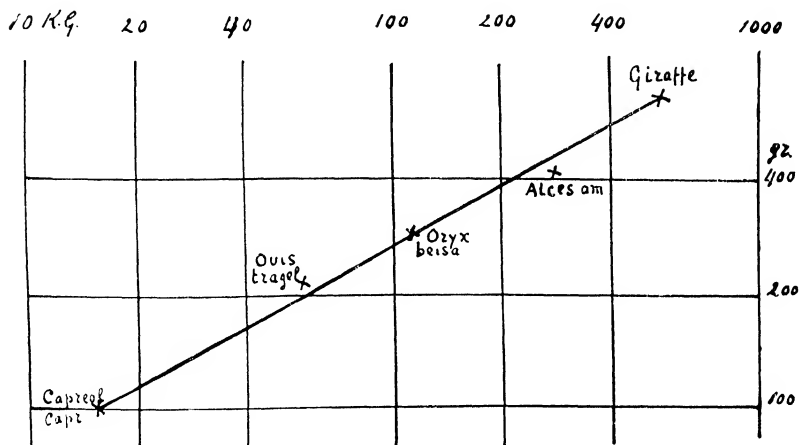
Fig. 107a. Graphic representation of the interspecial relation exponent in different Ungalates, by LAPICQUE.

the more so as LAPICQUE [2]) who, about the same time, also tested this exponent on mammals, came to the same result.

In 1905 LAPICQUE and GIRARD [3]) even found the same value for r (0,56) also in birds, while DUBOIS [4]), again, (1913) found it to

[1]) M. WEBER. Vorstudien über das Hirngewicht der Säugetiere. Festschrift f. Carl Gegenbauer Leipzig, 1896 and Verslagen der Kon. Akad. v. Wetenschappen, Amsterdam, October 1896.

[2]) LAPICQUE. Sur la relation du poids de l'encephale au poids du corps. Compte rendu de la Société de Biologie de Paris, Janvier 1898.

[3]) LAPICQUE et GIRARD. Poids de l'encephale en fonction du poids du corps chez les oiseaux. Compte rendu de l'Académie des Sciences. Tome 140, 1905. This paper is the more important as the authors give also the cephalization coefficients of different birds.

[4]) DUBOIS. On the relation between the quantity of brain and the size of the body in vertebrates. Proc. of the Kon. Akad. v. Wetenschappen, Amsterdam, Vol. 16, 1913.

hold equally good for all lower vertebrates. So apparently the exponential value 0.56 is a very fundamental figure in brain-body-weight relations.

LAPICQUE [1]) gave a very simple way of indicating graphically the exponent of relation by putting on an ordinate the logarithms of the brain weights, and on the abscissa the logarithms of the body weight
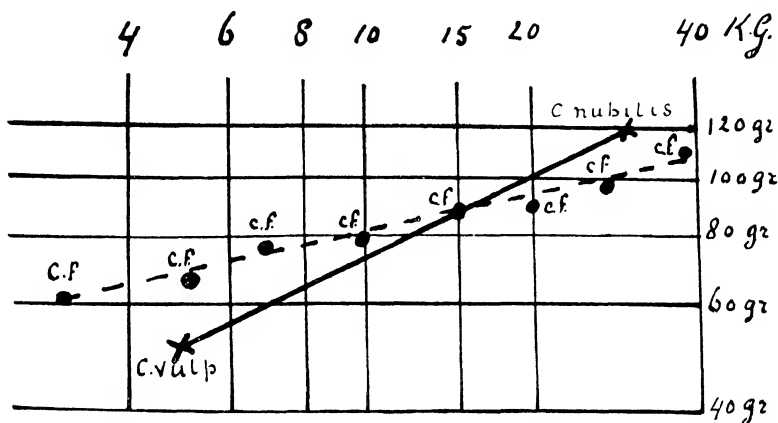
Fig. 107b. Graphic representation of the interspecial relation exponent in different Carnivora (full line) and the intraspecial exponent of different sized dogs (dotted line: c.f.), after LAPICQUE.

(fig. 107). The gradient connecting the exponents is practically a straight line, the *isoneural* whose angle with the abscissa is a function of the relation exponent, and consequently may be used on an indicator of it.

It appeared, however, to LAPICQUE (1898) and also to DUBOIS [2]) that the relation exponent (r) is much smaller (0.24—0.28) on using, for comparison, forms of *the same species*, e. g. dogs of different sizes

[1]) LAPICQUE. Tableau du poids encéphalique en fonction du poids corporel. Verhandl. des 7ten internationalen Physiologencongresses, Heidelberg, 1907. *The same*: Tableau general du poids somatique et encéphalique dans les espèces animales. Bull. Soc. d'Anthropol. 1908. See also the same: Le poids du cerveau et la grandeur du corps, Biologica, 2ieme année, No. 21, 1912.

[2]) DUBOIS. Ueber die Abhängigkeit des Hirngewichts von der Körpergrösse beim Menschen. Archiv. f. Anthropologie Bnd. 25, Heft 4, 1898.

(LAPICQUE [1])), or men of different sizes (DUBOIS [2]) and LAPICQUE [3])). In domesticated animals it is a little smaller (0.24) than in non domesticated ones (LAPICQUE, KLATT [4]), DUBOIS).

The remarkable fact that in comparisons among different sized individuals of the same species the exponent is about half as large as comparing different species, was explained by DUBOIS [5]), in agreement with the fact found by SUGITA [6]) in DONALDSON's laboratory, that among animals of the *same species* but differing in size (e. g. a terrier and a bulldog) there is practically only an increase of the *size* not of the number of the nerve cells in the larger individual, while in different sized species of the same order (e. g. cat and tiger) there is an increase in size as well as in number, so that the relation exponent is larger.

DUBOIS pointed out that the increase in size, occurring according to a potential 0,26, is not so far from the cytological nerve-cellbody volume potential, calculated from G. LEVI's [7]) and CONKLIN's [8]) data (0,31), thus confirming his supposition that the brain increase according to the exponent 0,26 may be due to enlargement of the ganglion cell without a considerable increase of their number.

The addition to this figure (0.26) to obtain 0.56 in interspecial comparisons might be due to the increase in the number of nerve elements [9]). As also in postembryonic growth the brain increase

[1]) See note 1, page 201.

[2]) See note 2, pape 201.

[3]) LAPICQUE. Le poids encéphalique en fonction du poids corporel entre individus d'une même éspèce. Bull. de la Société d'Anthopologie de Paris. Tome VIII, 5ieme serie, juin 1907.

[4]) KLATT. Studien zum Domesticationsproblem, Untersuchungen am Hirn, Bibliotheca genetrica. Bnd. II, 1921.

[5]) DUBOIS. Phylogenetic and ontogenetic increase of the volume of the brain in vertebrata. Proc. of the Kon. Akad. v. Wetensch. A'dam, Vol. 25, 1923, and DUBOIS. On the brain quantity of specialized genera of mammals Ibidem Vol. 27, 1924.

[6]) SUGITA. Comparative studies on the growth of the cerebral cortex. III and IV Journal of comp. Neurol. Vol. 29, 1918. See also DONALDSON. The significance of brain weight. Archives of Neurology and Psychiatry. 1925.

[7]) G. LEVI. I gangli cerebro-spinali. Suppl. all Arch. italiano di Anatomia e di Embriologia, Vol. VII, 1908.

[8]) CONKLIN. Body size and cell size. Journal of Morphology, Vol. 23, 1912.

[9]) It is remarkable that the part which the glia acts in the enlargement of the brain, is always left out of discussion. The glia probably behaves like connective cells, increasing chiefly in number in larger animals, not in size.

is chiefly due to an enlargement of the neurones DUBOIS called the intraspecial exponent (0,26) the *ontogenetic exponent,* while he called the interspecial exponent, occurring with different species (0,56), the *phylogenetic exponent.*

The intraspecial exponent actually is a little larger than 0,26 (between 0,26 and 0,28) but in domesticated animals, also in recent men (DUBOIS) it is smaller (0,22). This is interesting as in such animals also the cephalization coefficient is less than in wild ones of their sort (p. 204).

So far as concerns the relation exponents which only depend on quantitative somatic conditions.

As stated above this is not the only factor in establishing the weight of the brain. Another not less important one is the difference in intracerebral complexity, or cephalization which causes that a man has a much heavier brain than any animal of his size and even thrice as heavy as a Hippopotamus brain. Since, however, the general interspecial exponent is always 0,56 the difference due to *cephalization* can be easily calculated and expressed in a simple coefficient (k). Indicating the brain weight E. by the equation $E = k P^r$, the coefficient of cephalization k, appears to be nearly exactly the same among different species of the same genus, whose intracerebral complexity is the same — which are *homoneur* (DUBOIS) or *homocephalic* as one might say.

In brains that differ in intracerebral complexity, that are *heteroneur* — as DUBOIS expressed it — or *heterocephalic* as one might say, its value, calculated by the equation $k = \dfrac{E}{P^r}$ is larger for highly cephalized, and smaller for lowly cephalized animals.

If we thus calculate the k for a viverid, Paradoxurus musanga, and for the higher cephalized Lutra vulgaris (using, of course, the interspecial exponent 0,56) it appears that the k in Lutra is about twice as large as in Paradoxurus. In bears, especially the Malaybear, it is still larger; in anthropoids (0.75) it is again larger than in Carnivora (accept the Malaybear), in man it is largest of all (2,74).

The cephalization coefficient in various human races.

DUBOIS [1]) pointed out that the the cephalization, though varying but little in human races, is probably not exactly the same. This

---

[1]) DUBOIS. On the significance of the large cranial capacity of Homo Neanderthalensis. Proc. Kon. Akad. v. Wetensch. Vol. 23, 1921.

conclusion is based upon the fact that the average skull capacity in the Neanderthaloids is 1400 cM³. (BOULE), about the same as in present European races, while their body was smaller. The same obtains for some present races, as was already pointed out by SPITZKA [1]) for the Japanese, and as DAVIS stated for the Eskimos.

On the other hand Australians, Hindus and perhaps also some negro races have a relatively small skull capacity compared to the size of their body.

MANOUVRIER [2]) already stated that as a rule people with short and strong extremities and a strong musculature generally have a greater relative brain capacity as compared with those with slender long extremities and less developed muscles. DUBOIS is inclined to ascribe this to a better innervation and higher coordination of the muscular apparatus and proprioceptive sense.

He corroborated this view point by studies on the body brain weight relation among closely related animals. So comparing among platyrrhine apes the slow Mycetes with the active Ateles and Cebus he explains the about three times larger cephalization of the latter by its greater and more active muscular apparatus. Among anthropoids the Chimpanzee is about one third smaller than the Orang Outan while the weight of the brain is about the same. As there is no sufficient reason to accept great cognitive differences in these animals (SELENKA), DUBOIS supposes the larger brain bodyweight relation in the Chimpanzee to be a consequence of its greater pragmatic capacities, its greater muscularity and activity. The importance of activity is still more obvious in a comparison of the small but very agile Odontoceti with the larger but less agile Mysticoceti.

So DUBOIS supposes the same factor to cause the great cephalization of the Neanderthal race, and of the present Eskimos and Japanese.

In this connection I want to refer to the deteriorating influence of *domestication*, already visible in the *relation exponent* (p. 203).

On account of their researches LAPICQUE as well as DUBOIS, contemporaneously (1898 l. c. supra) but independently, stated that in all domesticated animals (rabbits, cattle, ducks) also the *cephalization coefficient* is smaller than in their non-domesticated relatives. In the

---

[1]) SPITZKA. The brain weight of the Japanese. Science Vol. 18, 1903.

[2]) MANOUVRIER. Sur l'interpretation de la quantité dans l'encéphale. Mémoires Soc. d'Anthrop. de Paris, 2ième serie, Tome 3, 1885, Quoted from DUBOIS (l. c. supra).

dog the decrease caused by domestication may be even 10% of the brain weight (DUBOIS [1])).

As domestication generally leads to a deterioration of independent activity, it does not seem improbable that similar differences as occur in animals, on account of their lesser pragmatic endowments, may be brought about gradually in the human race by the unnaturely deteriorating influence of domesticated life, which cannot make us expect a higher cephalization but a smaller one in those human races that have been for ages subject to such influences.

If there is also a difference in cerebral complexity caused by greater cognitive endowments, independent from pragmatic ones, among human races is very difficult to state.

To examine this, we should take groups in which in all probability the muscular apparatus and motile endowments do not differ very much. Perhaps Australians, Hindoes, Negroes and may be some European groups would provide material fit for comparison. This much is sure, that for such a comparison we should have perfectly trustworthy weighings of normal brains, and bodies done in the same way, in the same state of moisture, and preferably by the same person.

These points are specially emphasized by DONALDSON and his school (l. c. p. 198) and realized also by Dr. I. KELLERS PUTNAM in her comparative weighings of total brains and cerebella [2]) Everyone who personally has dealt with this matter knows what a difference it makes if brains are weighed with or without the leptomeninx. It is not only the leptomeninx itself, but the amount of fluid included in it that may make a great deal of difference.

It should be further stated whether the brain was weighed in a fresh condition, or after preservation, and if so in which fluid, and for how long.

On account of the fact that sometimes brains can be properly weighed only several days or weeks after death I would propose to accept as a standard to weigh brains, all meninges stripped, either fresh or after at least 4 months hardening in 10% formaline, the stem being cut at the calamus, and to mention whether or not the ventricles are emptied which makes an average difference of 34 gr. (HARVEY). The latter method enables us to use also a good deal of museum material.

This is the way I followed in weighing Chinese and Dutch brains. It gave me for fifty male Southern Chinese of Hongkong an average figure of 1239 gr., for Dutch males 1322 gr., both figures being lower than those mentioned by other authors (for the male Southern Chinese CLAPHAM BROWN mentions

[1]) DUBOIS. Bijdragen tot de Dierkunde. Amsterdam. Aflev. 22, 1922.

[2]) I. KELLERS PUTNAM. The proportion of cerebellar to total brainweight in mammals. Proc. Kon. Akad. v. Wetensch. Amsterdam, Vol. 31, 1928.

an average of 1385 gr. for 16 individuals which is probably too high, considering the skull capacities (REICHER, HABERER). RAUBER KOPSCH mentions 1332 gr., HARPER 1306 gr., KURZ [1]) 1407 gr.; for Amsterdam males BOLK [2]) found 1400 gr., DYKSTRA [3]) for Groningen (northern part of Holland) 1445 gr.

It is specially difficult to obtain good weight figures for the body as bodies weighed in hospitals are often emaciated and their weight by no means represents an average healthy individuals weight. For some races, e. g. the Chinese we now have excellent average weight, and height figures for the Northern, Central and Southern Chinese. Anthropology is much indebted to Dr. P. STEVENSON [4]), for this but this does not hold good for many non-European races.

Some authors, especially MOLLISON [5]) and HAUGER (l. c. infra), realizing these difficulties, have proposed to do away with brain and bodyweights, and to use skull and skeleton capacities, the latter expressed by the volume of the six most important bones of the right arm and leg (humerus, radius, ulna, femur, tibia, fibula) as an indicator of body shape.

There is much to be said in favor of this method, specially as it enables us to compare prehistoric with historic races. MOLLISON used this method with Gorilla material, HAUGER [6]) with men. The latter found an average skull-skeleton relation exponent in man of about 0.25, which shows that this method may give results analogous to the brain body weight method.

HAUGER examined skeletal material of different races and compared the skull skeleton capacity of twenty Australians with other races, among them Europeans. Supposing the same bodily functions to

---

[1]) KURZ (l. c. infra), weighed only two males (1545 and 1360 gr.).

[2]) BOLK. Petrus Camper. Deel II, 1904.

[3]) DIJKSTRA, l. c. infra.

[4]) STEVENSON. Collected anthropometric data on the Chinese. China medical Journ. Vol. 39, No. 10, 1925.

[5]) MOLLISON. Die Körperproportionen der Primaten. Morph. Jahrb. Bnd. 42, 1910.

[6]) HAUGER. Der Gehirnreichtum der Australier und anderer Hominiden, beurteilt nach ihrem Skelet. Anatom. Hefte Bnd. 59, Heft 179, 1921.

The fact that HAUGER finds a lower skullcapacity in the Australian than DAVIS, TURNER and DUCKWORTH may be a consequence of his method which gave him also a lower capacity in the European than is generally stated. This does not interfere much in his comparison.

be present in Australians and in those Europeans, he explained the differences as due to a different degree of intellectual cephalization.

HAUGER controlled his results by applying another method: Taking a constant percentage of the skeleton volume as an indicator for the volume to be taken from the skull capacity for somatic functions, he considered the rest of the skull capacity (which differed), as an indicator of cephalization [1]).
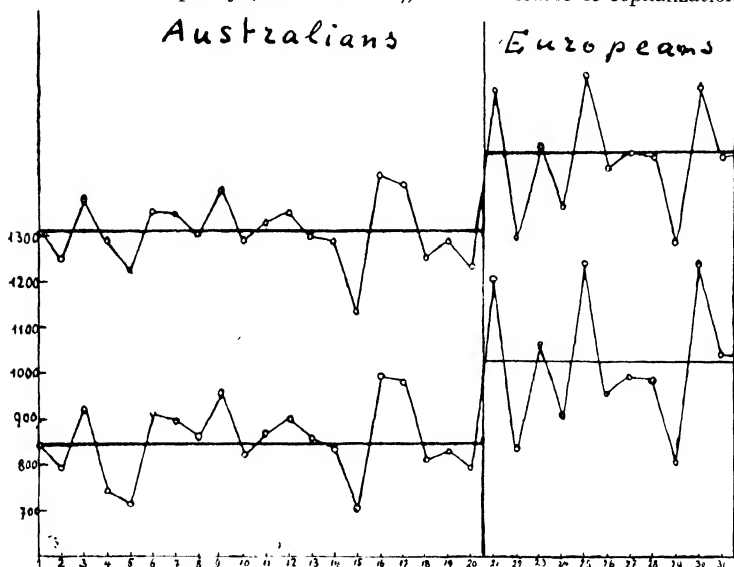
Fig. 108. Australian and European (German) cephalization curves after HAUGER. The upperline refers to the coefficient of cephalization calculated with equal exponent r, the lower refers to HAUGERS psychic component, calculated with equal somatic skeleton-skull volume.

In figure 108 I reproduce part of his results.

HAUGER concluded that there is a smaller intellectual cephalization in Australians than in Europeans. Although in HAUGER's work [2]) there are some mistakes, it is another expression of differences in cerebral complexity among various races, although the question

[1]) HAUGER also realized the necessity that we should only compare races of which we have sufficient evidence that the somatic factor is the same. Therefore he also considered the fact that in domesticated human races the bones are generally bulkier than in non domesticated ones.

[2]) E. g. in his statement that the relation exponent decreses gradually in the series from monkeys and anthropoids to man.

Among anthropoids this exponent is 0.56 as it is among non anthropoid

of pragmatic capacities should also be considered here (vide supra), — not only the cognitive intellectual. —

We may approach the problem of cephalization in human races still in another way by calculating the cord percentage on the brain weight taking as a limit either the calamus, as is customary, or, which may be better, the hind border of the pons.

Considering the great individual variation in the cerebellum-cerebrum percentage in animals (KELLERS PUTNAM) as well as in man (KAPPERS) it might be still better to sever the brain right in front of the cerebellum and to weigh pons plus cerebellum apart by cutting the stem behind the pons. We thus might establish the cord percentage on the forebrain plus thalamus and midbrain on one hand, and, on the other, the cord percentage on the cerebellar mechanism.

Comparative weighings with the calamus as a limit, in animals chiefly, have been done by RANKE [1]), who also determined the weight of the eyes in his material.

RANKE's figures are very interesting and the more trustworthy as he stripped the meninges and cut the nerve roots, including the cauda equina.

The following table gives some of his results:

Material.	Eye percentage of brain weight.	Cord percentage of brain weight.
Man (two specimens).	1.13%	2.03% } 2.41
Dog...............	11.88%	22.77%
Horse	18.40%	40.45%
Cow..............	15.78%	47.08%
Rabbit	60.62%	46.02%
Chick.............	108.82%	55.90%
Haddock..........	1323.53%	100.00%

RANKE further showed that the size of the individuals also plays an important part in this relation, the cord percentage in smaller animals of the same genus being smaller than in the large.

monkeys, whereas the smaller exponent, is also obtained among different dogs. (Cf. LAPICQUE's graphic fig. 107b).

[1]) RANKE. Zur Anthropologie des Rückenmarks. Arch. f. Anthropologie, Bnd. 23, 1895.

Also MIES [1]), ZIEHEN [2]) and PFISTER [3]) gave us comparitive brain cord weight figures.

DONALDSON [4]) discussed the influence of sex on this relation; (in male Germans 1.96%, in female Germans 2.01% after MIES [5])).

From the figures gathered by these authors it appears that, while man has not the greatest relative brainweight as compared to the body [6]), no animal in which these relations are hitherto established has a lower cord percentage than man.

Unhappily data for the brain cord relation in various human races do not exist in literature, as far as I know, and a good many weight relations in each race have to be gathered to obtain trustworthy averages. This would be, however, very valuable, especially if the three parts of the central nervous system as mentioned above were weighed separately.

If all those who have the opportunity to gather figures from European, or foreign races would do so, mentioning the sex, age and body length, we might soon have very valuable figures for this purpose.

Influence of cephalization coefficient and body size on brain form.

In animals of the same order, e. g. Paradoxurus and Lutra, a greater cephalization also influences the general morphology of the brain.

Studying the influence of the cephalization coefficient on the

---

[1]) MIES. Das Verhältnis des Hirnszum Rückenmarksgewicht etc. Centralblatt f. Anthropologie, Ethnologie und Urgeschichte, 1897.

[2]) ZIEHEN. Das Nervensystem in Bardelebens Handbuch der Anatomie des Menschen. G. Fischer, Jena, 1899.

[3]) PFISTER. (Zur Anthropologie des Rückenmarks Neurologischen Zentralblatt, 1903) gives only figures of human material up to 6½ years.

[4]) DONALDSON. A comparison of the albino rat with man in respect to the growth of the brain and the spinal cord. Journ. of Comp. Neurology, Vol. 18,1908.

[5]) Also PFISTER found that from birth to maturity the weightrelation between brain and spinal cord in man is always slightly more in favor of the brain than in woman, although in comparison to body length the spinal cord weight in boys is always somewhat more than in girls, which probably has to be explained by the boy's greater muscular development.

[6]) The bodyweight relation in man is about 1 : 33, but in some small animals the relative brainweight is higher; in the marmoset it is 1 : 22, in the capuchin 1 : 13 and in the humming bird 1 : 12. See: DORSEY. Why we behave like human beings, HARPER and BROKERS, New York and London.

general form of the brain [1]), *I found that invariably all those animals
of an order that have a distinctly higher cephalization coefficient
are more brachencephalic or less dolychencephalic* [2]) *than those of
that same order, whose cephalization is less.*

Instead of ciphers, which may be found in my original communi-
cation on this subject, I give two figures, which clearly illustrate
this fact. Fig. 109 shows the brain of the viverid Paradoxurus, and
that of the mustelid Lutra. Both are Carnivora, but the latters
cephalization is about 1½ times as large as the former's (DUBOIS).
It is evident that its brain is broader, the length-width index of
the fore brain of Paradoxurus being 76,2, that of Lutra 86,2.

Paradoxurus musanga,   Lutra vulg. adult (nat. size).
   adult (nat. size).
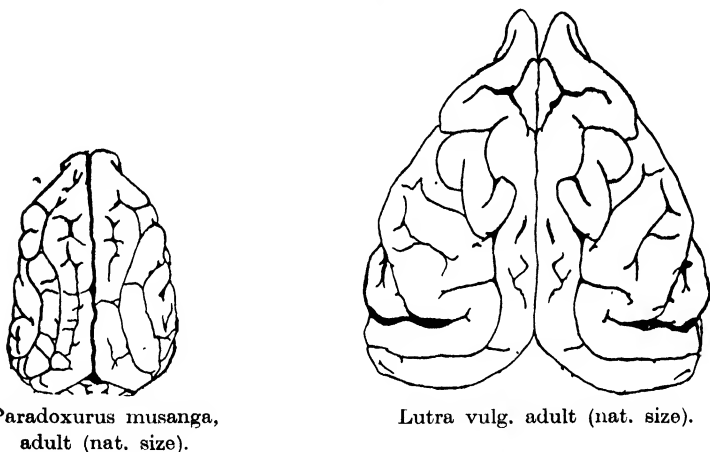
Fig. 109. Brains of two Carnivora showing dolichencephaly in the lower
     and brachencephaly in the more highly cephalized animal.

The same holds good for Nasua and Ursus maritimus. While the
cephalization of the latter is about twice as much as that of Nasua
(DUBOIS), the length width index of Nasua brains is only 72 and

---

[1]) ARIËNS KAPPERS. The influence of the cephalization coefficient and
body sizes upon the form of the forebrain in mammals. Proc. of the Kon.
Akad. v. Wetensch. Amsterdam. Vol. 31, 1927.

[2]) The expression brachy- and dolichocephaly is used for skulls, the expression
brachen- and dolichencephaly for brains. If length width endices are mentioned
below and the skull is not specially mentioned they always refer to brains
or endocranial casts.

that of Ursus maritimus 92. So I could give a great many examples in all orders of mammals.

The explanation of this fact is very simple. The more highly cephalized brain, surpassing the increase parallel to size has to acquire a rounder i. e. a more voluminous shape in consequence of its increasing more than is compatible with the original headform (the latter being part of the body).

I may add to this that not only does the relative *width* of the brain increase in the more cephalized animal, but also its relative *height*, provided no special factors counteract it.

So the brain approaches the form of a globe, because this has the greatest content for the smallest surface.

It further appeared to me that the rounding and the compression of the brain, resulting from this, is not without influence on the form and position of its sulci. So the circumsylvian sulci in Ursus arctos and maritimus, whose cephalization (0,5) is about $1\frac{1}{2} \times$ as high as that of dogs (0,37, DUBOIS [1])) are more compressed than in the dog. The ecto-sylvian fissure, lying outside the pseudosylvia in the dog, lies in the sylvian fissure in bears where the insular region consequently is more opercularized. This is still more striking in Ursus malayanus, whose cephalization (cf. DUBOIS [1])) even equals that of anthropoid apes (0,75). The same holds good if we compare Paradoxurus and Lutra. In the latter even the anterior suprasylvian fissure may enter the Sylvia [2]).

So greater cephalization in mammals may lead to brachencephaly and to pronounced fissural consequences.

This, however, does not mean that brachencephaly is always due to greater cephalization (vide infra p. 216 and 217).

On the other hand, in animals of the same species or genus the *influence of a larger body size on the form of the brain is the opposite of the influence of greater cephalization.* Among different sized animals of the same species or family, and equally cephalized, the larger animals

---

[1]) DUBOIS. The significance of the large cranial capacity of Homo Neanderthalensis. Proc. Kon. Akad. v. Wet. Vol. 23, 1921.

[2]) For the topography of these sulci as for a survey of the phylogenetic development of sulci in general I refer to my book: Vergleichende Anatomie des Nervensystems der Wirbeltiere und des Menschen, Vol. II, Bohn, Haarlem, 1921 and my report on cerebral localization and the significance of sulci, at the XIIIth international congres of medicine, London, 1917.

Fig. 110. Brain of Cervulus muntjac. (nat. size).
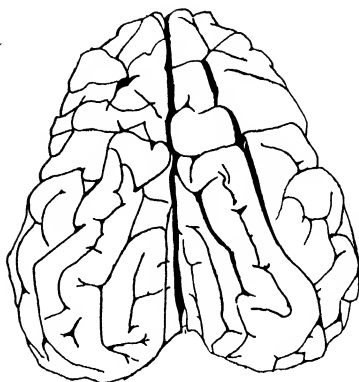
Fig. 111. Brain of Rucervus duvauceli. (nat. size).
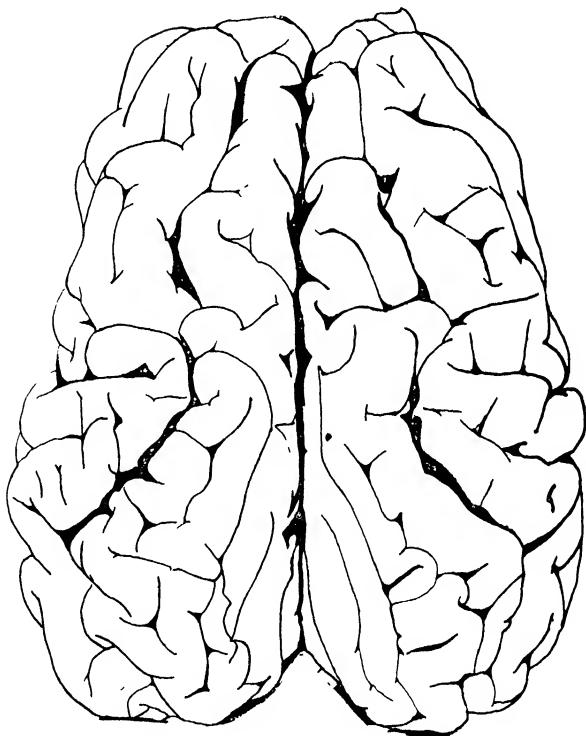
Fig. 110 and 111. Showing a dolichencephalic brain in a large animal and a brachencephalic brain in an equally cephalized smaller animal of the same group (Cervidae).

are more dolichencephalic than the smaller, a fact demonstrated already for long in the skull by KLATT and others, (l. c. supra).

Fig. 110 and 111 show the brains of two equally cephalized animals of the same family (Cervidae).

Rucervus duvauceli is dolichencephalic (77,5) while the Muntjac is brachencephalic [1] (85.8).

The difference in the form of the brain of small and larger animals of the same species is apparently very much the same as observed between young (newborn) and adult individuals of one species (see figs. 112 and 113).

Sus scrofa dom. neon.   Sus scrofa dom. adult.
(nat. size).   (nat. size).
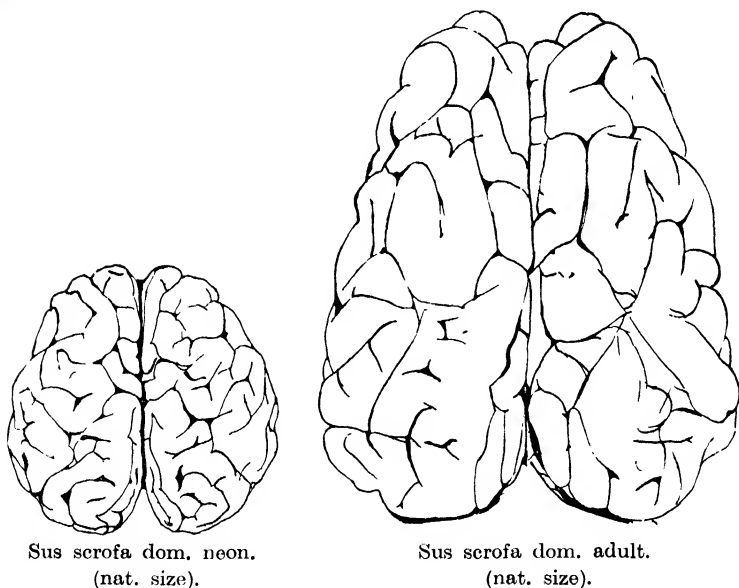
Fig. 112. Showing a greater brachencephaly in the smaller, newborn pig (91.4) than in the larger, adult pig (81).

Consequently if an animal of the same species or genus is larger, or grows larger, its brain (and skull) increase in length more than in width.

Dolichencephaly *may* thus be explained by assuming that an animal is a large representative of its genus, *which, again, does not*

---

[1]) Sometimes the smaller animal's brain is only less dolichencephalic (not necessarily brachencephalic). My index figures refer to the forebrain only.

include that all dolichencephalic animals are large representatives of their family, because there are also other, e. g. external factors that determine the form of the skull (see below) and of the brain.

To this I may add that in the smaller or younger animal not only the relative width but also the relative height of the brain *may be* greater than in the larger animal.

It is self-evident that in the longer brains also the fissures are more stretched, less compressed, and tend less to opercularization.

I mention these facts, because the indices of skulls and endocranial casts act an important part in anthropology and the factors that *may* determine these indices as far as they depend on the brain, are much easier demonstrated — also in their consequences on fissuration — in animals than in man, because in the animal series the variety in cephalization as well as in body size is so much greater than among man.

Also exterior factors influence the general form of the skull and consequently the general form of the brain. Amongst these are a strong development of the jaw muscles (which makes the skull narrower) and of the neck muscles (which extend it backward), further the influence of food, domestication, etc. [1].

Now it is striking that nearly all anthropoïds are brachencephalic (the average for the Chimpanzee is 84—85, for the Orang Outan 87 [2]), for the Gorilla, see below), more so than the other large katarrhine monkeys (including the Gibbon) which have an average length-width index of about 80.

This probably has to be correlated with the fact that the Chimpanzee and Orang Outan are more cephalized than the lower katarrhine monkeys, their cephalization index being about twice as large as that of the latter (with the Orang also other factors — mechanical ones — influence its brachencephaly).

On the other hand the brain of Pithecanthropus has an index of 81 and primitive human skulls hitherto found are mostly mesen-

---

[1] A short but valuable enumeration of these factors is given by BASLER Die Beeinflussung der Schädelform durch die Umwelt, Deutsche medizinische Wochenschrift No. 43 and 44, 1925. — See also DUBOIS. On the cranial form of Homo neanderthalensis and Phithecanthropus erectus determined by mechanical factors. Proceed. of the Kon. Akad. van Wetensch. Amsterdam, Vol. 24, 1922.

[2] If not mentioned otherwise, the indices given are measured on the brain, or on endocranial casts or cavities, not externally on the skull.

cephalic, or subbrachencephalic. Only in later (Azilian) ages, introducing the neolithic period, exquisite brachencephalic men appear in Europe [1]) (vide infra).

What does this mean? There are several hypotheses, but we have no certainty about any of them. So it is certainly remarkable that also among the *Gorillas* great variations occur. Although the endocranial index of most Gorillas is brachencephalic (average 82, HARRIS; 84.4 COUPIN), HARRIS [2]) found variations from 72 to 86,2, and also BOLK [3]) measured one specimen of 72,2.

The Gorilla is the only living anthropoid in which meso- and even dolichencephalic brains occasionally occur, but DART's fossil Taungs Chimpanzoïd had also an index of 72.

It seems not probable that primitive men are related to the Gorilla. Human ancestry is certainly of older stock than that of the present living Gorilla. DART [4]) supposes his Chimpanzoïd fossil Austrolopithecus africanus (Taungs ape) to be akin to man e. g. on account of its dolichencephaly. Others — among whom DUBOIS — believe that man's ancestors may have been related with fossil Gibbons (index 80). Of living apes the Chimpanzee is probably nearest to man.

Though the shape of DUBOIS' Pithecanthropus in some respects resembles that of the Gibbon, in most respects it is more Chimpanzoïd (SCHWALBE, WEINERT). Its frontal fissuration certainly resembles that of the Chimpanzee more than that of any other anthropoid [5]).

The cephalization coefficient in Pithecanthropus, however, is certainly twice as large as in anthropoids, and in Neanderthalmen about four times larger (DUBOIS). According to this, we might expect Pithecanthropus to be more brachencephalic than anthropoids and Neanderthalmen more brachencephalic than the ape man from Java, *if* anthropoids, Pithecanthropus and man were closely related,

---

[1]) At Ofnet in Bavaria in one tomb brachycephalic and dolichocephalic skulls are found, the former are considered by BOULE as alpine the latter as mediterranean by SCHLIZ. Among the earlier skulls only those of Krapina are slightly brachycephalic but not so exquisite as the Bavarian (Ofnet) skulls.

[2]) HARRIS. American Journ. of physical Anthropology, 1926.

[3]) BOLK. Proc. of the Kon. Akad. v. Wetensch. Amsterdam, 1925.

[4]) RAYMOND A. DART. Australopithecus africanus, Nature, February 1925.

[5]) ARIËNS KAPPERS. The fissures on the frontal lobes on Pithecanthropus erectus DUBOIS' compared with those of Neandelthalmen, Homo recens and Chimpanzee. Proceed. Kon. Acad. v. Wetensch., Amsterdam, 1929.

the more so as the body size of the latter (calculated from the femur) was about equal. As, however, the Neanderthaloïds generally have a lower encephalic index than that of the Pithecanthropus such a *close* relation is very improbable.

And why does exquisite brachencephaly in Europe only appear more recently? Did those exquisite brachencephalics originate elsewhere [1]) as brachencephalics, or is it possible that a prevailing mesenencephalic race mixed with a few spells of brachencephalics gradually developed into a brachencephalic form on account of the well known heriditary dominance of brachencephaly?

We have no answers on all these questions. So much is sure that with these exquisite neolithic brachencephalics we do not have a phenomenon comparable to what is observed among animals, viz. that the rounding of the brain is due to a higher cephalization coefficient- or to a smaller bodysize. The brain-body weight relation, even in recent brachencephalics, is not higher than in primitive mesenencephalic man, and in present living dolichencephalic and brachencephalic human races the brain quantity is about the same, perhaps even a little smaller in the latter.

DYKSTRA [2]). confirming SCHWERTZ' [3]) statement for Germans, found that also in the Dutch the *optimum skull capacity* (not a larger relation exponent) occurs with men as well as with women at a skull index (measured externally) of 78, which approximately corresponds to an encephalic index of 79,5 or 80.

Now it is interesting that an encephalic index between 78 and 81, often occurs with Neanderthal men, and that their brainvolume is also very remarkable even for a recent race. The exquisite brachencephaly in some later races thus has to be explained by other factors than higher cephalization or smaller body size since brachencephalic races, extinct or living, were not shorter than the mesencephalic Neanderthal man.

---

[1]) It is probable that these early European brachycephalics came from central Asia, but this is only a displacement of the difficulty, since the oldest skulls hitherto found in Central Asia are dolichencephalic or mesencephalic. See BLACK: The prehistoric Kansu race.

[2]) DYKSTRA. Bijdrage tot de physische anatomie van schedel en hersenen. Geneeskundige bladen uit kliniek en laboratorium, 1927. Firma Erven F. Bohn, Haarlem.

[3]) SCHWERTZ. Die Alamannen in der Schweiz. Zeitschr. f. Morphologie and Anthropologie. Bnd. 14, 1912.

As according to Dubois the relatively long shape of the Neander-
thaloid skull is largely influenced by muscle actions (note 1 p. 214) the
probable decrease of these factors [1] may have favored brachence-
phaly, the more so since newborns among all races tend to brachen-
cephaly and brachencephaly is predominant in heredity upon
dolichencephaly. This together with Bolks fetalization theo·y (see
below) might perhaps give an explanation here.

ENCEPHALOMETRIC INDICES.

Before proceeding to a further analysis of racial differences in the human
brain, I shall give a brief exposé of the indices which I introduced for this
purpose, most of which I first applied for studies on the Chinese brain, but
which appeared to be also useful in comparisons between anthropoids and man
and for the study of endocranial casts of prehistoric skulls.

Till now the general morphology of the endocranium is expressed by skull
measurements, as calotte height, bregma angle etc.

It is however desirable to have also indices and index lines based upon the
encephalon itself. For this purpose one may measure on the cast or on well
fixed brains the greatest transverse diameter and the greatest length (brain
index), further the relation between the diameter at the orbital opercula
(greatest diameter of the frontal lobe) and the greatest diameter of the temporo-
parietal region, which divided upon each other give an index comparable to
the width index of the skull basis (cf. Martin's Anthropology). The sagittal
indices are more easily measured on photographs of the lateral and (for actual
brains) of the mesial wall of the hemispheres. For this the brains should be
preserved by injection of formol in the carotids or suspended by the basil
artery in a wide jar before being halved.

On these *photographs* the following lines are drawn:

Laterally:

1. A line connecting the basis of the operculum orbitale with the basis of
    the lobus occipitalis: the *lateral horizontal*. On this line the following
    perpendiculars are traced:
2. the perpendicular along the anterior pole of the frontal lobe: *frontal
    perpendicular;*
3. the perpendicular along the anterior pole of the temporal lobe: *insular
    perpendicular;*
3a. the perpendicular reaching the basis cerebri immediately in front of
    the optic chiasma at the recessus praeopticus: *chiasma perpendicular;*
4. the perpendicular from the highest point of the centro-parietal lobe:
    parietal perpendicular;

---

[1] Appearing from the decrease of supraorbital ridges and other muscle
insertions.

5. the perpendicular along the posterior pole of the occipital lobe: *occipital perpendicular;*
6. the perpendicular from the utmost ventral point of the temporal lobe: *temporal perpendicular;*

M e d i a l l y: (for actual brains only):

7. The line connecting the basis of the splenium with the basis of the genu corporis callosi: the *basal callosum line;*
8. the perpendicular from the highest point of the corpus callosum upon this line: the *callosum perpendicular;*
9. the line between the most frontal and most caudal points of the external periphery of the callosum: the *callosum length* [1]).
10. A line parallel with the bottom of the fourth ventricle, running to the basal callosum line: *the stem axis.*

In using these lines, which should be measured with the nonius, the following indices may be calculated [2]):

A. The *general height index* of the brain, being the parietal perpendicular, divided by the lateral horizontal.

B. The *occipital index*, being the parietal perpendicular, divided by its distance to the occipital perpendicular.

C. The *temporal depth index*, being the temporal perpendicular, divided by the lateral horizontal.

D. The *temporal length index*, being the distance from the insular perpendicular to the occipital perpendicular, divided by the lateral horizontal [3]).

E. The *frontal height index*, being the chiasma perpendicular, divided by the lateral horizontal [4]).

F. The *frontal length index*, being the distance from the chiasma perpendicular to the frontal perpendicular, divided by the lateral horizontal [4]).

G. The *callosum index*, being the callosum perpendicular, divided by the callosum length.

---

[1]) In most of my photographs this line is drawn over the whole cerebrum, in order to measure also the distance of the frontal and occipital pole of the brain to the callosum.

[2]) In the calculation of height indices of the encephalocranium it is customary to multiply the perpendicular with 100. It might be better not to do so with the brain indices, so as to distinguish skull and brain indices immediately.

[3]) The temporal length index was not yet introduced in my paper of 1926.

[4]) In my paper of 1926 the frontal height and length indices were calculated by the insular perpendicular, being divided, in E by its distance from the frontal pole, in F by the lateral horizontal, but I there already remarked that thus calculated they gave no adequate expression of the frontal length and height of the brain as the place of the insular perpendicular varies with the frontal outgrowth of the temporal lobe, which, especially in fetusus and neonati, is a very varying factor and does not express anything about the frontal lobe but only about the temporal lobe. The insular perpendicular is now used only for expressing the relative length of the temporal lobe in the total length of the brain.

H. The *stemangle*, being the frontal angle between the stemaxis and the basal callosum line.

I. The lateral horizontal, also permits a measurement of the *dorso-ventral extension of the rostrum orbitale*, that in recent man shows a varying extension underneath this line, but in primitive man (see the La Chapelle aux Saints, Rhodesian and Australian cast) already begins dorsal to the lateral horizontal and in Anthropoids extends largely above this line (fig. 113).

The temporal perpendicular prolonged in a dorsal direction over the lateral surface may also be used to measure the inclination of the Sylvian and central sulcus, two points repeatedly discussed in literature, (CALORI, HAMY, HARE, EBERSTALLER, CUNNINGHAM), to which, however, very little attention is given in recent times when more is forgotten than taught in matters of general brain morphology. CUNNINGHAM [1]) whom we owe so much measured each of these inclinations in a different way. His Sylvian angle (opening *dorsally*) was measured between the average course of the stem of the f. Sylvii and a perpendicular on the longest axis of the brain, thus differing only slightly from my Sylvian angle (see below). His Rolandic angle (opening *frontally*) however was measured between the average course of the central fissure and the tangent on the brain dorsum where the Rolandic fissure indents the mesial wall. Consequently CUNNINGHAM's Rolandic angle enlarges if the central fissure runs more perpendicular, while his Sylvian angle enlarges if the Sylvian fissure runs more horizontally.

My system has two advantages over CUNNINGHAM's:

1⁰. both angles are measured on one perpendicular and both angles enlarge the more the fissures in question deviate horizontally.

2⁰. as the angles are measured on the same perpendicular the interfissural inclination between the Sylvian and Rolandic fissure may also be easily calculated by subtracting the acute Rolandic angle from the less acute Sylvian.

Figure 113 demonstrates my method in anthropoids [2]).

CUNNINGHAM and some of his predecessors got results that are well worth mentioning.

So CUNNINGHAM could not confirm CALORI's statement that the length-width index of the brain has a marked influence on the Sylvian angle. He found, however, that his *Sylvian angle* (which is nearly the same as mine) increases from a full time fetus to adult life from about 64° to about 70.3° as a consequence of the downgrowth of the parietal and central region (cf. my new born, fig. 139, with the dolicho- and brachycephalic Dutch, fig. 133 and 135). An other interesting result of his measurements is that in apes (where the average

---

[1]) CUNNINGHAM. Contribution to the surface anatomy of the cerebral hemispheres. Cunningham Memoirs No. VII publ. by the Roy. Irish Acad. Dublin, 1892.

[2]) If the central sulcus is not clear enough in its entire length on a photo, the top of the axis of this sulcus may be indicated with Chinese ink on the brain itself before taking the picture.

is 50°) as well as in man he found the Sylvian angle somewhat larger on the left than on the right hemisphere. He ascribes this to a preponderance of the parietal region on the left side, evident in man by his righthandedness (l. c. p. 135—136). I also found the Sylvian angle to increase after birth, even more than 6°.

CUNNINGHAM found his *Rolandic angle* to be very constant after the 8th month of fetal to adult life when it is about 71.6° on an average. EBERSTALLER found the Rolandic angle to vary in the adult from 70° to 75°. My experience with the Rolandic angle is that it acquires its definite position only about the 5th month after birth. In fetuses CUNNINGHAM's Rolandic angle is *larger* and in conformity herewith, my Rolandic angle is *smaller* since in fetuses and in anthropoids the central fissure is still further removed from the horizontal tangent and has a more perpendicular course. CUNNINGHAM found that his angle probably *increases* with the caphalic index. Similarly my Rolandic angle *decreases* with this index [1]).

My *inclination angle* between the two fissures decreases during development, my Rolandic angle increasing more than my Sylvian angle [1]).

— -   - -

[1]) This seems to hold good as well for Dutch dolichencephalics as for the Dutch brachencephalics. In the Chinese however this inclination angle seems to be generally larger (see p. 284).

PREHISTORIC BRAINS.
The Pithecanthropus brain.

Few relics of prehistoric human brains have been found. Only some disseccated prehistoric Egyptian brains have been described by ELL. SMITH [1]), who also gave us a report about a disseccated Tasmanian brain [2]). But all these specimens belong to neolithic or even historical periods. Of more primitive men no petrified or disseccated brains are found (T. EDINGER [3])). For the brain morphology of extinct races we are restricted to endocranial casts, which mainly inform us about the general contours of the brain, sometimes only about its upper part as in many cases the basis of the cranium fails, and thus the total height of the brain and the position of the stem (foramen magnum part) to the rest of the encephalon cannot be deduced from it.

This is also the case with DUBOIS' *Pithecanthropus erectus.*

DUBOIS stated that the Pithecanthropus is a tertiary, late pliocene creature, an opinion sustained by many other anthropologists, among whom KEITH. K. MARTIN and VOLZ are inclined to believe that the stratum in which it was found is quaternary and already contains remains of man (molars), Nowadays the layer is generally considered, also by DUBOIS, as a pleisto-pliocene transition.

Formerly considering it as a link between apes [4]) and man DUBOIS recently stated, that it has a nearer relationship to the Gibbon: "it is not a transition of any type of manlike apes to the human

---

[1]) ELLIOT SMITH. On the natural preservation of the brain in the ancient Egyptians, Journ. of Anatomy and Physiol. Vol. 36, 1902.

[2]) ELLIOT SMITH. Le cerveau d'un Tasmanien. Bull. et mém. de la soc. d'authropologie de Paris, déc. 1911.

[3]) Dr. TILLY EDINGER. (Versteinerte Menschen-Hirne aus der Eiszeit: Natur und Museum-Heft 7, 1927. Frankfurt a/Main), doubts the fossil character of the brainlike silicates described by HINDZE (Mitt. der Anthrop. Gesellsch. in Wien. Band 67, 1911) and considers them to be purely anorganic formations. See also HINDZE: Les cerveaux pétrifiés fossiles. Mém. de l'Institut International d'Anthrop. IIIième Congrès. Amsterdam 1928.

[4]) For descriptions of anthropoid brains I chiefly refer to TILNEY and RILEY: The brain from ape to man; MINGAZZINI Morphologie der äuszeren Grosz-hirnhemisphärenoberfläche bei den Anthropoiden. Arch. f. Psychiatrie, Bnd. 85, 1928; LE GROS CLARK, The cerebral hemispheres of a Gorilla. Journ. of Anat. vol. 61, 1928; BURNE and ELL. SMITH's Catalogue of the Roy. Coll. of Surgions, and RETZIUS' Affenhirn.

type", he says, but "the agreement of the skull with the anthropoid cranial type, specially Hylobates, is striking"[1]).

Others — SCHWALBE[2]), WEINERT[3]) and myself (l. c. infra) — consider the Chimpanzee as its nearest anthropoid relative.

The lengthwidth index of the cast (81.2) comes however nearer to that of the Gibbon (H. syndactylus) which has an average of 80 (see fig. 113 : 79.7) the index of most Chimpanzees — though varying considerably — being as an average much higher (85).

Although the skull is not more highly arched and has no less receding forehead than in Hylobates, there is no doubt that the brain was enlarged far beyond the homoneuric ratio of anthropoids. Estimating its body size after its femur the cephalization of Pithecanthropus is about twice as much as in the Gibbon (DUBOIS).

Its endocranial capacity according to DUBOIS is 900 cc.m., according to Mc. GREGOR[4]) about 940 cc.m., according to WEINERT, it is at least 1000 cc.m. Considering the fact that dry skulls always have a somewhat smaller volume than fresh ones, we may probably add to this 30 cc.m. Taking the brain volume to be 91% of the skull capacity this volume would be about 937 cc.m. which, with a spec. weight of 1,037, would give a brain weight of 972 gr., which is much more than that of the greatest present living anthropoids (HAGEDOORN's[5]) largest Gorilla skull had a capacity of 655 cc.m.) and only 200 gr. less than the average (male and female) brain weighth of the Australians.

In the endocranial cast of the Pithecanthropus the basis, and the orbital surface of the brain are lacking. This is the more regrettable as these parts may be of importance, on account of the extent of the orbital keel (rostrum), so conspicuous in anthropoids (see fig. 113).

Also the ventral part of the temporal lobe fails, and most of the cerebellum. Still, what is left is of utmost importance.

---

[1]) DUBOIS. On the principal characters of the cranium and the brain, the mandible and teeth of Pithecanthropus erectus. Proc. of the Kon. Akad. v. Wetensch. Amsterdam, Vol. XXVII 1924 and ibidem: Figures of the calvarium, endocranial cast, etc. of Pithecanthropus erectus (page 269).

[2]) SCHWALBE. Studien über Pithecanthropus erectus Dubois. Zeitschr. f. Morphologie und Anthropologie. Bnd. I, 1899.

[3]) WEINERT. Pithecanthropus erectus Dubois. Zeitschr. f. Anatomie und Entwickl. gesch. Bnd. 87, Heft 3 und 4, 1928.

[4]) Mc. GREGOR. Natural History. Vol. 25, 1925.

[5]) HAGEDOORN. Anat. Anzeiger Bnd. 60, 1925—1926, p. 417.

Troglodytes gorilla, after TILNEY and RILEY.

Pithecanthropus erectus DUBOIS (for fiss. see text).

Hylobates syndactylus (Gibbon).

Pongo pygmaeus (Orang utan).

Troglodytes niger (Pan spec.; Chimpanzee).
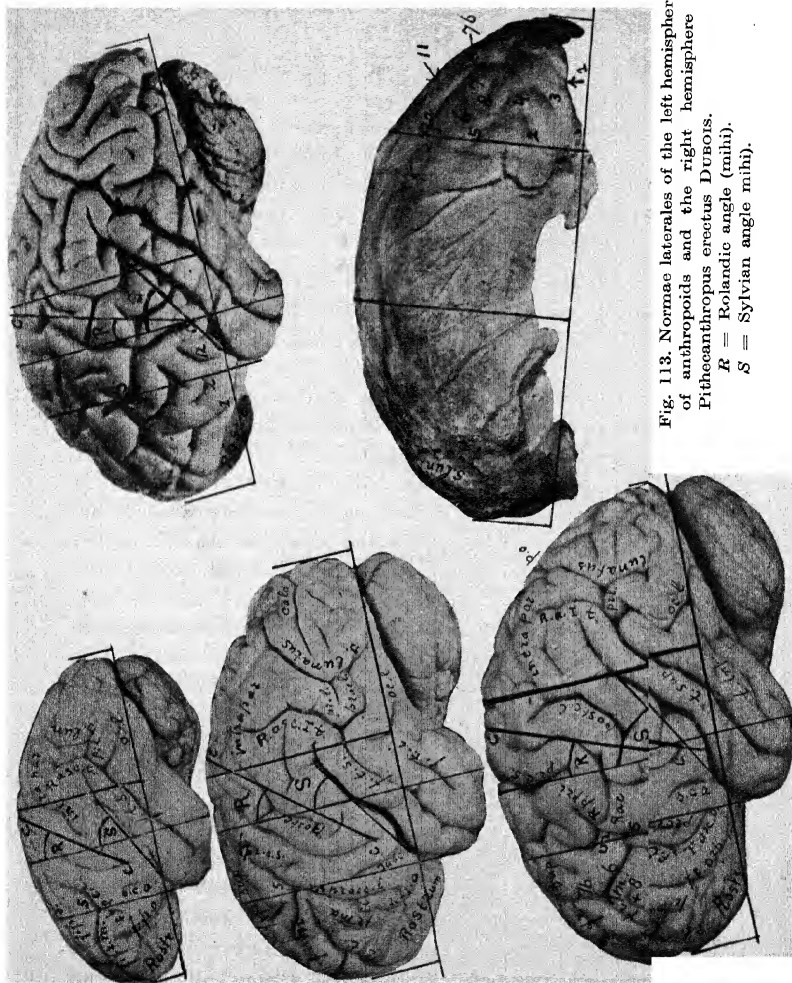
Fig. 113. Normae laterales of the left hemispheres of anthropoids and the right hemisphere of Pithecanthropus erectus DUBOIS.
R = Rolandic angle (mihi).
S = Sylvian angle mihi.

Brain Indices.	Hylob.	Orang.	Chim-panz.	Gor. cast.	Pithec-anthrop.	Pilt-down Keith rec.	Neand. Rhod.	Dutch dolich.
General height.	0.415	0.514	0.530	0.444	0.400	0.498	0.450	0.491
occ. index.....	1.04	1.83	1.41	1.04?	0.938	1.465	1.110	1.190
temp. depth...	0.158	0.178	0.173	0.224	?	0.137	0.142	0.145
temp. length..	0.748	0.751	0.721	0.721	0.753	0.711	0.766	0.748
front. length...	0.397	0.429	0.420	0.356	0.344?		0.332	0.346
front. height...	0.443	0.516	0.487	0.444	0.422?		0.450?	0.443
call. index.....	0.330	0.375	0.295	0.294	?		?	0.321
Stemangle.....	131°	1.27°	135°	133°				106°

As the sagittal aspect of the calotte shows a great resemblance with Hylobates (DUBOIS) also my endo-cranial indices show a greater conformity with those of the Gibbon brain than with the Chimpanzee's (see the above list).

It is however immediately striking that, seen from above, in Pithecanthropus the frontal lobe is blunt, while in Hylobates (as in the Gorilla) it is more or less pointed (fig. 114). In this respect Pithecanthropus resembles more the Chimpanzee.

Also the fissuration of the frontal lobe is more Chimpanzoid (vide infra). On the rest of the cast only the lunate sulcus is indicated with a sufficient degree of probability, corresponding, on the right hemisphere with the top of the lambda suture (see also p. 229). Behind it the posterior calcarine and a part of the occipitalis superior of ELL. SMITH (ypsiliformis mihi, triradiatus LANDAU) is seen. On the left the lunate sulcus may lie more backward, but is less evident (cf. also ELL. SMITH l. c. p. 229, and plate IV).

The fissuration of the frontal lobe is much more complicated than that in Hylobates, whose frontal fissures have a very simple character and are less numerous (fig. 113). They resemble more those in the Chimpanzee (fig. 115), as also the skull does according to SCHWALBE, and WEINERT. A single *ramus anterior fossae Sylvii* (2) is clearly present on the right hemisphere (perhaps also on the left [1])) in front of the subcentralis anterior (12). Besides the *fronto-orbital* fissure, or what seems to be its homologue, is present, running however less far on the convexity than in anthropoids. I shall call this fissure which in a similar form occurs in human races, the *f. subfrontalis* (1).

---

[1] This cannot be stated with certainty as of the left lower part of the lobe too much is lacking.

The *inferior frontal sulcus*
(4) makes a wider arch on
both sides in the Pithe-
canthropus than in this
Chimpanzee. As however
also in Pithecanthropus
this arch is smaller on the
left than on the right side,
nothing can be said about
a special development of
the left subregio frontalis
inferior of BRODMANN,
(which in man contains the
speech centre), in Pithe-
canthropus.

As appears from fig. 115
the *frontalis medius* (7) on
the right hemisphere of the
ape-man resembles the one
on the left side of this
Chimpanzee very much.
Only the space between the
inferior and midfrontal fis-
sure is larger in the apeman.

The *sulcus frontalis me-
dius* (7) of Pithecanthropus
extends between the top
of the *fronto-marginalis* (9)
and the *praecentralis in-
ferior* (5) as it does in
the Chimpanzee, having in
both a dorsal, hooklike
convexity. On the right of
Pithecanthropus as on the
left of this Chimpanzee the
junction (6) of the frontalis
medius and precentralis lies
just in front of my insular
perpendicular (fig. 113).
From this junction the prae-

Fig. 114.

Dusseldorf Neanderthalman

Pithecanthropus

Chimpanzee

Tilney's Gorilla

Hylobates
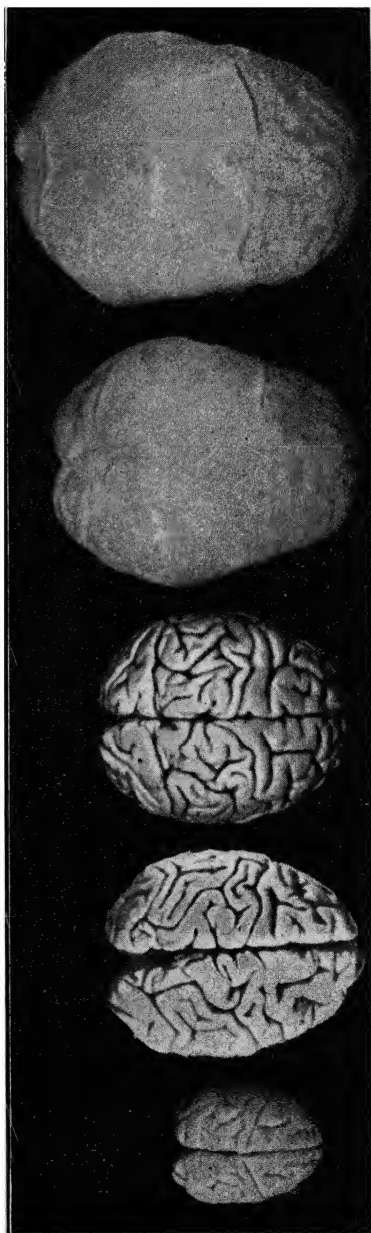
centralis inferior runs further dorsally (5a) in both the Pithecan-
thropus and Chimpanzee. On the right of Pithecanthropus as on
the left of this Chimpanzee from the arch of the frontalis medius

Chimpanzee.
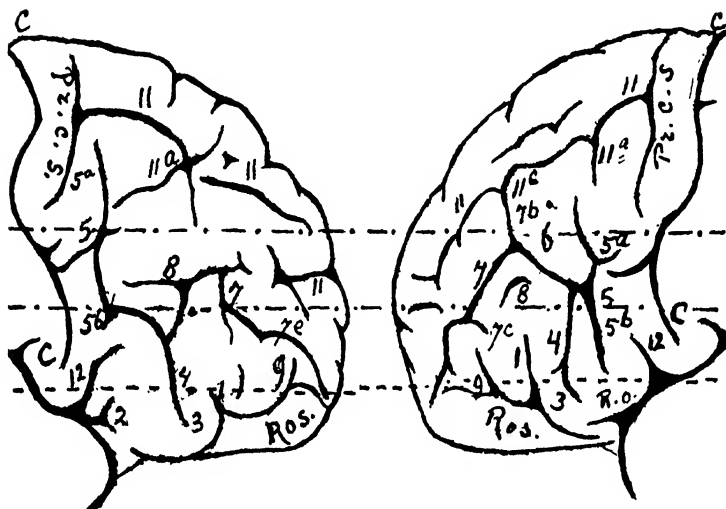
right lobe   left lobe
Pithecanthropus
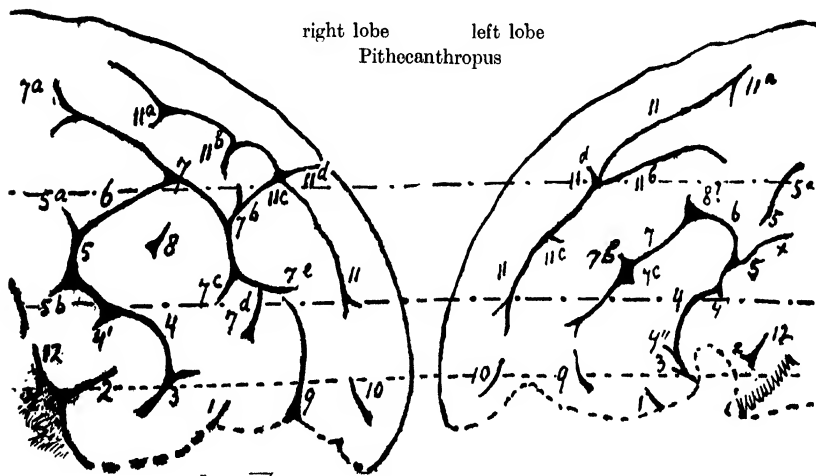
Fig. 115.
Frontal lobes of a Chimpanzee and of Pithecanthropus erectus.

Plate IV.
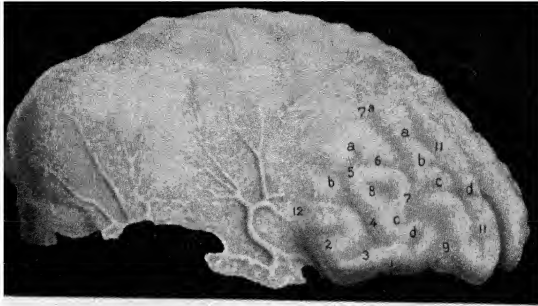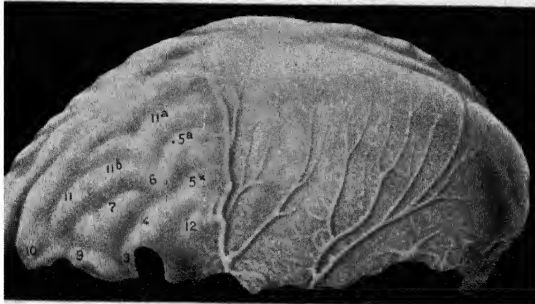
Vlassopoulos' drawings of the endocranial cast of Pithecanthropus erectus Dubois. In the middle figure behind and under 9 (which refers to the fronto-marginal sulcus in front of it) also a vestige of the fiss. subfrontalis (1) is seen.

a dorsal branch (7*b*) connects with the *frontalis superior* (11).
The larger part of the *frontalis superior* is clearly indicated and
has some other *descending branches* (11*ᵃ* and 11*ᵇ*), not connecting
with the frontalis medius, similarly as 11*ᵃ* in the Chimpanzee.

While the frontalis medius or the left side of Pithecanthropus runs some-
what lower than on the right, the wider space between this fissure (7) and
the frontalis superior (11) contains a much longer branch of the latter (11*b*).

The *central sulcus* is not visible as perhaps only ventrally on the
right hemisphere by a short deepening some distance behind 5*b*,
near the subcentralis anterior (12) and just in front of the anterior
branch of the arteria meningea media (not numbered; see plate).

So the frontal lobes compared to that of the Chimpanzee chiefly
show a frontally more stretched course of the sulci, as is in
harmony with the fact that the Pithecanthropus brain is less
brachencephalic (81,2) than this Chimpanzee's (86,2).

Furthermore the foot of the midfrontal convolution (between 7
and 6) is larger in Pithecanthropus.

Though the gyr. frontalis inferior is enlarged on both sides, it is
less enlarged on the left than an the right. As on both sides only
traces of a single ram. anterior fossae Sylvii occurs, we have no
morphological evidence for assuming a specially developed operculum
frontale and speech centre [1]) on the left hemisphere [2]).

The *temporal width* corresponding with the posttemporal region
(see p. 148) is so striking in Pithecanthropus that, seen from above
(fig. 114), the cast has more or less the form of a trigonum [3]).

While the *frontal and posttemporal* region, are probably more deve-
loped in this creature than in living Anthropoids, the greatest in-
crease seems to occur in the *parieto-occipital region*, as already

[1]) Speech as many suppose, originates in producing emotional and imitative
sounds, faculties, however that also occur in several animals. See G. BAUMANN:
Ursprung und Wachstum der Sprache; Oldenbourg, München, 1913.

[2]) In recent man the left gyrus frontalis inferior is usually a little larger
than the right and a single ram. anterior fossae Sylvii, though it may
occur on both sides, is less frequent (11°/₀) on the left than on the right (41°/₀;
CUNNINGHAM, QUANJER).

[3]) This lead DUBOIS to believe that the animal was to some degree trigono-
cephalic, l. e. that its frontal bones are prematurely fused. DUBOIS concludes
to this precocious fusion from a slight torus medianus frontalis.

appears from the fact that the length relation of the parietal bone (DUBOIS) to the frontal bone and the squama of the occipital is greater in Pithecanthropus than in Anthropoids (though smaller than in men). So, although the lunate sulcus (on the right) corresponds with the lambda suture, it lies much further backward than in apes. This points to a shifting backward of the visuo-sensory area on account of an increase of the stereognostic and visuo-psychic area, which may be still greater on the left than on the right hemisphere [1]).

Whether or not we have to consider Pithecanthropus as a direct predecessor in human ancestry, this much is sure that by these features, and also by its brainweight (taxed on about 970 gr.) and cephalization coefficient (p. 222), it stands between the greatest recent Anthropoids (max. brainweight less than 600 gr.), and man (average of European men and women 1300 gr. of Australian dito 1160 gr.).

The Piltdown cast.

Very little can be said of the Piltdown cast. The reconstruction made by KEITH (fig. 115 A) gives it an endocranial length-width index of **79.1** a capacity of 1330 ccm. Its sagittal indices are given on p. 224. From this appears that it differs very much from the Pithecanthropus cast, but also from Neanderthal casts.

No fissures may be observed on it with certainty. For further details I refer to KEITH (l. c. see p. 228), and to ELL. SMITH [2]), who supposes that its capacity was no more than 1200 c.c.m. This much is sure that these relics are much more human than those of Pithecanthropus and that they may

Fig. 115 A. Endocranial cast of the Piltdown (Eoanthropus Dawsonii) reconstruction by Sir ARTHUR KEITH.

represent the dawn of humanity, a chellean man of the inferior pleistocene.

[1]) For a more detailed description I refer to my paper in the Proc. of the Kon. Akad. v. Wet. Amsterdam, 1928. to KEITH's Galileereport, and to:

[2]) ELL. SMITH. The Evolution of Man. Oxford Univ. Press. 1927.

The brain of Neanderthal men.

The endocranial casts of the Neanderthal race show great variations in their length-width index.

So while the *La Quina* woman is distinctly dolichencephalic: 73.8 (ANTHONY [1])), the *Düsseldorf* and *La Chapelle* [2]) man, according to ANTHONY, have an encephalic index of 78.3 and 78.8. According to my own measures the Düsseldorf man had even a somewhat greater index viz. 79.6 equal to that of the *Gibraltar* woman (79.5) which according to ANTHONY [3]) even has an index of 81.6.

Also among the *Krapina* skulls [4]) brachencephalic indices are found, and the endocranial cast of *Podbaba* is certainly brachencephalic (I tax this to be about 84.5).

The brains of Neanderthalmen were much larger than that of Pithecanthropus, about equally large as recent human brains.

Contrary to what was supposed by BROCA [5]) and BUSCHAN [6]), a noteworthy increase of average skull capacity from this prehistoric race to later men cannot be stated (RÖSE [7])), although some Neanderthaloid skulls have a small capacity (e. g. Rhodesian: 1260 ccm.).

The same has been emphasized by G. RETZIUS [8]) for the last ten centuries. This author found the average male skull çapacity of the Swedish in the stone age to be 1489, the average in the iron age 1497 and in the present age 1452.

The endocranial capacity of the Neanderthalman of La Chapelle aux Saints is even 1600—1626 ccm. (BOULE), which is more than the average capacity

---

[1]) ANTHONY. l'Encéphale de l'homme fossile de la Quina. Bull. et Mém. de la Soc. d'Anthropologie de Paris, 1913.

[2]) BOULE et ANTHONY. l'Encéphale de l'homme fossile de la Chapelle aux Saints. l'Anthropologie6 Vol. 22, 1911.   [3]) Ibidem.

[4]) BOULE. Les Hommes fossiles.

[5]) BROCA's reaearches really concerned recent men, as he compared 115 Parisian skulls of the twelfth century with 242 more recent skulls of different epochs. See: Sur la capacité des crânes parisiens des diverses époques. Bull. de la Soc. d'Anthrop. de Paris, Tome III, 1862.

[6]) BUSCHAN. Archiv für Rassen- und Gesellschafts Biologie, Bnd. I, 1904, and Gehirn und Kultur, Wiesbaden 1906.

[7]) RÖSE. Beiträge zur europaeischen Rassenkunde. Archiv. f. Rassen- und Gesellsch. Biologie, Bnd. II und UUU, 1905, 1906.

[8]) RETZIUS. Wächst noch die Grösse des menschlichen Gehirns infolge der Einwirkung der Kultur. Zeitschr. f. Morph. und Anthrop. Bnd. XVIII, 1924.

of recent Europeans. So· in the Dutch (DYKSTRA, l. c.) the male skull capacity is 1545 for dolichocephalics, 1577 ccm., for mesocephalics, and 1515 ccm. for brachycephalics. For women these figures are 1335, 1370 and 1355 cm³. As average capacities for both men and women this gives 1440, 1473 and 1435. About 91% of this capacity is brain volume.

Also the capacities of the *Düsseldorf* (1400 DUBOIS [1])), *Gibraltar skull* [2]) (1296 BOULE [3])) Spy II (1600, DUBOIS [1])) and the skull of *La Quina* (1367 [2])) and Rhodesia (1260) fall to the average of recent Europeans.

If with BOULE we take the average skull capacity of all adult Neanderthalmen and women to be about 1400 cM.[3], perhaps some but only very little difference [4]) with the recent European may have occurred.

Besides by estimating the Neanderthalmans bodyweight after his distinctly smaller skeleton it appears that his cephalization is at least the same, perhaps even a little larger, according to DUBOIS, than in recent man.

Although the general shape of the casts shows a good deal of difference with recent man, there is, however, a still greater difference between Neanderthal casts and that of Pithecanthropus. From the latter the Neanderthal cast differs not only by its skull capacity but also by its greater height indices (see page 224) and broader *frontal lobe*, so that the frontal width of the brain contrasts less with the temporal width (fig. 114), than it does in Pithecanthropus.

In comparison with recent brains the *frontal and occipital height indices* are smaller and the *temporal lobes* (fig. 117), may have been more turned inside though not as much as in Anthropoids. Another feature is the more pronounced impression in the ventrolateral margin of the temporal lobe, caused by the os petrosum, which gives the frontal part of the temporal lobe a more independent character (fig. 116 B), still more pronounced in some Anthropoids (e. g. Orang utan) and in the Piltdown cast (fig. 115 A).

The rostral keel (rostrum orbitale) and the juxtarostral concavity of the orbital surface, caused by the large orbits, is larger than in the recent European (see Rhodesian and La Chapelle cast, plate V and VI).

---

[1]) DUBOIS. On the significance of the large cranial capacity of Homo neanderthalensis. Proc. Kon. Akad. v. Wetensch. Amsterdam, Vol. 23, 1921.

[2]) These may have belonged to females.

[3]) BOULE. l'Homme fossile de la Chapelle aux Saints. Annales de Paléontologie, 1911.

[4]) The less so as dried human skulls have about 50 cm.[3] less capacity than fresh ones (see p. 222).
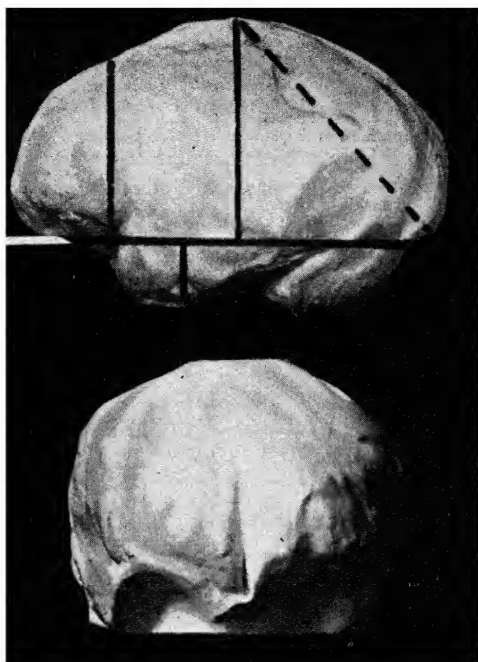
Fig. 116 A. Lateral and frontal aspect of the La
Chapelle aux Saints cast after M. BOULE. Note the
orbital keel lying mainly dorsally to the lateral
horizontal as it does in apes (fig. 113).

Fig. 116 B. Endocranial cast of the Rhodesian
skull. Note the large orbital keel beginning
dorsally to the lateral horizontal.

The *juga* and *impressiones digitatae* on the innerside of the skull,
so pronounced in some lower mammals (not, however, in Anthropoids)
and even in Pithecanthropus, in Neanderthal men become less distinct.
SYMINGTON [1]) showed that in recent man they may be still less distinct.

Still in some of the Nean-
derthal endocranial casts
the fissures on the orbital
and frontal lobes are suffi-
ciently clear to allow a
comparison with the Pithe-
canthropus and recent man.
Fig. 117 shows the basal
aspect of the Rhodesian
brain in which besides the
blunt temporal lobe, and
large orbital rostrum, the
orbital fissures are very dis-

Fig. 117.
Orbital fissures and subfrontal fissure in
the Rhodesian cast.

tinct. It shows the presence of the sulc. olfactorius, the internal
and external orbital sulcus, forming with a transverse fissure
the "incisure en *H*" of *Broca*. Lateral to this is a well ex-
pressed *subfrontal fissure* surrounding the operculum orbitale as
it does in Pithecanthropus (1). In fig. 118 the lateral fissuration
of the frontal lobes is seen. While the *superior frontal fissure* (11)
is less distinct caudally, *Eberstallers frontalis medius* (6,7) is clearly
expressed [2]). On the right side of the Düsseldorf man it shows a striking
resemblance to the same fissure on the right lobe of Pithecanthropus.
Here and in the La Quina cast (*left*) it reaches the *fronto-marginal* (9).
On the *left* frontal lobe of the Düsseldorf and La Chapelle man the
frontalis medius (7) clearly resembles the same fissure on the *right* lobe
of the Rhodesian having a ventral offshoot 6', pointing to or connec-
ting with the *intermediate fosset* 8 or even with the *frontalis inferior* (4).

A great variety is observed in the *inferior frontal sulcus*, which
on the *left* lobe of the La Chapelle man and La Quina woman in
addition to a *ramus inferior* has also a *ramus anterior* (r. ant.), not

---

[1]) SYMINGTON. On the relation of the inner surface of the cranium to the
cranial aspect of the brain. Edinburgh medical Journal, Febr. 1915. See, however,
also BOULE and ANHHONY: Neopallial morphology as studied from endocra-
nial casts. Journ. of Anat., vol. 51, 1917.

[2]) Concerning this fissure see footnote 3 on p. 263 and 264.

Fig. 118. Fissures on the frontal lobes of the Neanderthal man from Düsseldorf (D.), La Chapelle aux Saints (La Ch.), La Quina (La Q.) and Rhodesia (Rh.); *l* = left hemisphere, *r* = right hemisphere.

Plate V.

Occipital aspect of the endocranial cast of the Düsseldorf Neander-thalman. Note the lunate sulcus behind the lambda suture on the left hemisphere.

Right hemisphere of the Rhodesian cast; 9 refers to the fronto-marginal sulcus behind it.

Plate VI.
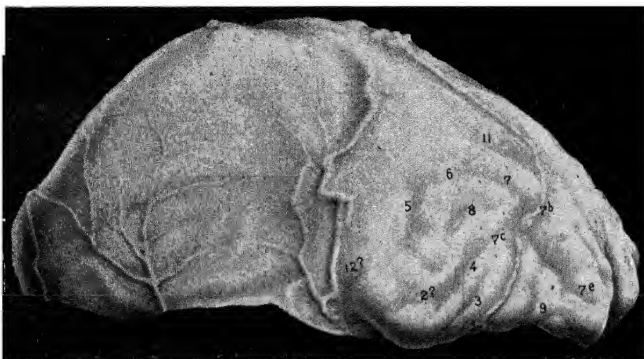
Dussel-
dorf cast

La Quina
cast
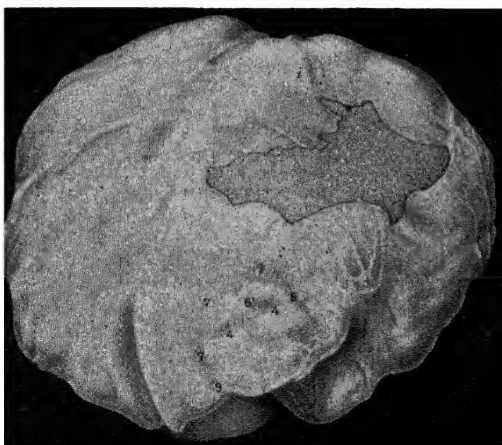
La Chapelle
cast

occurring in the Pithecanthropus nor in the Chimpanzee. Although a trace of this ramus anterior may be indicated also on the right hemisphere of the La Quina and Rhodesia casts it is striking that in the Neanderthalmen hitherto examined it is best pronounced on the left lobe. In Homo recens, under this fissure, partly also under its anterior branch lies the subregio frontalis inferior of BRODMANN which on the left acts a part in speech. In comparison to Pithecanthropus the *inferior frontal convolution* has enlarged dorsally and frontally [1]).

The *frontomarginal fissure* (9) is clearly indicated and so is the *subfrontalis* (1), which surrounds the ventral end of the ram. inferior fiss. frontalis inferioris. Two *rami anteriores fossae Sylvii* limiting a distinct operculum frontale are nowhere seen, nor a *fiss. axialis operculi frontalis*. The former may be indicated by 2? on both sides of the Düsseldorf cast and on the right of the Rhodesian and left of the Chapelle cast. The *subcentralis anterior* (12), always lying behind and below the praecentralis (in contrast to the former) is perhaps indicated on the Düsseldorf and La Quina casts where perhaps also a part of the central sulcus (just in front of the anterior branch of the arteria meningea media) may be indicated (c. ?).

The lunate sulcus, supposed to exist on both sides of the La Quina cast by ANTHONY, is only clearly visible behind the sutura lambdoidea on the left occipital lobe of the Düsseldorf cast, where it shows a similar relation as may be observed in recent men (Plate V).

I strongly doubt wether the semicircular impressions immediately in front of this suture in the Rhodesian skull, described by ELL. SMITH, are lunate sulci. Their frontal position, exact correlation with the lambda suture. and great symmetry lead me to think that they probably are caused by a thickening of the hind border of the parietal bone, occurring occasionally also in recent men.

Concerning the *stem* it may be stated that in those Neanderthaloids where the basis of the skull is well preserved, the slope of the craniovertebral plane is more oblique than in recent man which indicates that the *stem angle* of the oblongata to the brain though much less

---

[1]) On both sides of the Düsseldorf cast the inferior frontal sulcus is interrupted in its horizontal course by a posterior and anterior frontal bridging convolution (also described in recent men, EBERSTALLER), connecting the inferior with the midfrontal convolution behind and in front of the intermediate fosset 8, which thus acquires an arched shape on these lobes.

obtuse than in anthropoids runs more obliquely than in recent man. This is probably a consequence of the more stooping attitude of the Neanderthalman's head which causes the foramen magnum to lie more caudally. This same stooping attitude of the head on the vertebral column may have favored the occipital elongation of the skull, on account of the stronger force of the occipital muscles (NYSTRÖM, THOMSON) and perhaps also its flat form (DUBOIS [1])).

I may add that similar relations of the frontal fissures as described here were found by KEITH [2]) in the *Galilee* cast.

The endocranial cast of the *Rhodesian* fossil has very much the same features as those of the other Neanderthal casts.

The main difference with the other Neanderthalmen is, that the brain is a little higher, less platycephalic.

The large rostrum, however, extends further ventrally to the lateral horizontal than in the La Chapelle cast. Finally the foramen magnum lies a little more frontally (BOULE), thus pointing to a somewhat less stooping position of the head and less obtuse stem angle.

The capacity of the skull is however small (1280 cc.m., WOODWARD SMITH) and the inferior frontal sulcus, having no distinct ram. anterior is rather simple. I found a similar relation of this sulcus in an australian aboriginal's brain and KEITH draws a similar relation on an australian aboriginal's cast. He and RAMSTRÖM consider this skull as being more primitive than European Neanderthalmen.

Resuming we may say that Neanderthal brains are more primitive than recent human brains by being more flat, having a pronounced orbital keel starting far above the lateral horizontal, a concave orbital plane, a large petrosal impression, a long occipital and rather blunt temporal lobe the anterior part of which has a deep ventral extension.

The fissures of Neanderthalmen differ from those of Pithecanthropus, by showing a distinct dorsal and frontal enlargment of the inferior frontal convolution, an increase of the foot of the midfrontal convolution and backward shifting of the lunate sulcus.

---

[1]) DUBOIS. The form of the Neanderthal skull explained by mechanicul factors. Proc. Kon. Akad. v. Wetensch.

[2]) Report on the Galilee skull. Publ. of the British school of Archeology in Jerusalem. London, 1927.

The stem angle is larger than in recent men but smaller than in apes.

In Neanderthalman *unidexterity* is supposed to have existed not only on account of a slightly larger length (some further backward protrusion) of the left hemisphere in some Neanderthalmen, also occuring in recent races (WEINBERG [1]), but chiefly on account of a larger weight of his right humerus (BOULE, l. c. 232).

ELL. SMITH [2]) has added to this that, similarly as in recent man, the lunate, if present, is more conspicuous on the left than on the right, which I can confirm (cf. plate V). He is inclined to explain this as being due to a greater crowding in the left parieto-occipital area in connection with righthandedness.

It is interesting, however, that K. H. BOUMAN, who personally tested the fitting of prehistoric impliments of MOUSTIER in his right and left hand, found about an equal number fitting left as well as right, whereas with Solutrean implements the right hand prevails.

The question of the different size and weight of the two hemispheres is a difficult one and the results are not very conclusive, even in recent man.

BROCA and THURNAM believed the right hemisphere to be the heavier one, BOYD the left. According to CRICHTON BROWNE it differs with age, the left being heavier between 40—60 years, the right under and above that age. FRANCESCHINO, WAGNER and BRAUNE found about an equal number of cases in which the left or the right were slightly heavier and in which both were practically equal [3]). A similar result was published by ORTON [4]) who weighed the hemispheres of 27 brains. J. VILDE [5]) who examined 200 brains, found that in 63% the right hemisphere was heavier; in 31,5% the left, while in 5,5% he found equal figures.

DONALDSON has rightly pointed out that the way of cutting the brain, which is necessarily arbitrary, may strongly influence the results.

Personal researches convinced me of the truth of this supposition, and further showed that the *cortex*, which is *naturally* (not artificially) divided into entirely

---

[1]) Cf. also ELL. SMITH. On the asymmetry of the caudal poles of the cerebral hemispheres and its influence on the occipital bone. Anat. Anzeiger, Bnd. 30, 1907. GORGIANOFF assumes the left hemisphere to be more vascularized.

[2]) ELL. SMITH. Right and lefthandedness in primitive man. Brit. medic, Journal, Dec. 1925 and: The evolution of man, Oxford University Press, 1927.

[3]) For references see my paper in the Proc. of the Kon. Akad. v. Wetensch. Amsterdam, Vol. 28, 1925. The relative weight of the brain cortex etc. (also (Journ. of nerv. and mental disease, 1926).

[4]) New England Journ. of medicine, Nov. 1928.

[5]) J. VILDE. Ueber das Gewichtsverhältnis der Gehirnhälften beim Menschen. Acta Universitatis Latuensis, Riga, 1926.

separate parts, is not constantly heavier on one side (l. c. 1927). This does
not necessarily imply that the thickness of all the cortical areae is the same
left and right. So LINDON MELLUS [1]) found in three brains the cortex of the
speech center in the third frontal convolution to be obviously thicker
(especially the supragranlar and granular layers) than at the corresponding
spot on the right hemisphere and he believes the same to hold good for the
acoustic center (superior temporal). GANS found that the middle third of the
post central convolution, corresponding with the sensibility of the hand, is
more constantly broader in the left hemisphere in Europeans than in the
Javanese, where frequently this centre in the right hemisphere is larger [2]).

This lower paleolithic or Neanderthal race, appearing already
before the third or Riss glacial period, was most abundant in Europe
in the third or last interglacial period. Though knowing the use of fire,
it may have lived largely on raw vegetables, as is made probable
by its teeth (DUBOIS), and has gradually disappeared from Europe
in the very long and severe last glacial and the cold post glacial
period, in which its feeding conditions got poorer and poorer.

It left only simple chipped inpliments, no paintings nor sculpture,
and had no elaborate death cult or totemism. Only the men of
Moustier, La Ferrassie and La Chapelle were given a simple burial.

The brain of upper paleolithic men.

The following or *upper palaeolithic races* that inhabited Europe
during the last glacial and post-glacial period is the *reindeer race* or
Homo sapiens fossilis, thus called because they are the creators of
beautiful mural paintings and sculptors of adorned ivory and bone
implements. Though no pottery nor polished implements are left by
them (these appear first in neolithic times) they had an elaborate
death cult and very pronounced totemism.

Several types or races of upper palaeolithic or reindeermen have
occurred. The earliest group are the Grimaldi negroids. Later
are the aurignacian Cro Magnon and Combe-Capelle man and the
solutrean Predmost race. Still later are the magdalenean skulls.

All, except the Placard skull, are dolichen- or mesencephalic.

---

[1]) LINDON MELLUS. A contribution to the study of the cerebral cortex
in man. Anat. Record. Vol. V, 1911.

[2]) GANS. Das Handzentrum in der linken hinteren Zentralwindung. Zeitschr.
f. d. gesamte Neur. und Psychiatrie, Bnd. 75, 1922. GANS observed a similar
contrast in 6—8 months European fetus and a Chimpanzee. See also Ibidem
Bnd 85, 1923.

Geological / archaeological timeline chart (rotated)

Epoch	Climate / Glaciers	Fauna	Years	Culture period	Geologic stage	Human type	High Art
ALLUVIUM HOLOCENE	CLIM. APPR. AS NOW	FAUNA REC. DOM. ANIM.	3500 / 5000	PROTOHISTOR — NEOLIT	BRONCE COPPER — H. MEDIT., ALPIN., NORDIC		POTTERY AGRIC MEGAL. MON. HUTS
DILUVIUM			10000	AZILIAN	MESOLIT. or EPIPAL.	OFNET	MARK. PEB. ST.
PLEISTOC. S	COLD POSTGLAC. PER.; WÜRM GLACIERS	STEPP-F., REINDEER, TUNDRA-F., BOS PRIM., BISON, EQUUS CAB.		MAGDALENEAN, SOLUTREAN, AURIGNACEAN	SUPERIOR H. SAP. FOSS. PALEOLIT	CHANCELADE, CRO MAGNON, PREDMOST BRN, AURIGNAC, GRIMALDI	MARKS: USE OF CLAY IVORY HORN BONE, PAINT. SCULP, HUNT. TOTEM, DEATH OR NAM; NOMADIC LIFE; BURIAL
			20000	MOUSTEREAN		LA CHAPELLE, MOUSTIER, LA FERRASSIE, SPY I AND II	CAVE DWELL.
PLEISTOC. M	INTERGLAC. PER.	MAMMOUTH, HYENA SP., URSUS SP., RHIN. TICH., FELIS LEO, EQUUS CAB.		" " "	INFERIOR PALEOLIT — HOMO NEANDER THALENSIS SIVE MOUSTERIENSIS	KRAPINA, PODBABA, LA QUINA, DUSSELDORF, GALILEE, RHODESIA	TOTEM?; NO PAINT... SCULPT.
			50000	MOUSTEREAN			
PLEISTOC. I	RISS GLACIERS; INTERGLAC. PER.	ELEPH. ANT., RHIN. MERCK, TROGONT	100000 / 200000	ACHEULEAN, CHELLEAN	PALEOLIT PRIMITIVUM	PILTDOWN, EHRINGSDORFF?, HEIDELBERG	FIRE
PLEISTO- PLIOCENE	MINDEL GLAC., INTERGLAC. P., GÜNZ GLAC.	HIPPOPAMPH, ELEPH. MER., RHINOC. ETR, EQUUSSTEN, HIPPOP MAJ, STEGODON	500000		EOLITHICUM OR NATUR. STONES	PITHECANTHROP. TRINIL, JAVA	SPEECH?; NO SPEECH VEGETARIAN

Fig. 119. Right hemisphere of the man of
Combe Capelle.
Note the greater height of the cast and
the smaller orbital keel.

A striking feature of all types compared to the Neanderthal men,
is the higher endocranial cavity and cast (fig. 119).

Brain indices.	Pithec.	Rhod.	Chap. aux S. (La [1] Quina)	Combe Cap.	Predm. 111, IV, 10 Average.	Marsh. Bush-women.	Austr. cast.	Dol. Dutch.	Brach. Dutch.
General height.	0.400	0.450	0.480 (0.465)	0.507	0.516	0.469	0.489	0.491	0.522
Occipital height	0.938	1.110	0.99 (1.10)	1.502	1.455	1.275	1.322	1.190	1.450
Temp. depth ..	?	0.142	0.153 (0.153)	0.121	0.140	0.137	0.132	0.145	0.160
Temp. length..	0.753	0.766	0.773	0.743	0.787	0.755	0.748	0.760	$\mp$
Front. length..	0.344?	0.332?	0.306?	0.350		0.362	0.356	0.346	0.363
Front. heighth.	0.422?	0.450?	0.437?	0.450?		0.408	0.426	0.443	0.473
Callosum......	?	?	?	?		0.320	0.332	0.321	0.382
Stemangle.....						104°	105½°	106°	100¹/₃°

1) The indices of the La Quina cast, are in brackets.

Related, in most cases, with the greater height of the brain is the steeper slope of the occipital and frontal lobe.

In the adjoining list I give the sagittal brain indices of Pithecanthropus, some lower paleolithic or Neanderthal men, some upper paleolithic men and some recent races. From this it appears that in all the upper paleolithic men the general height index is larger, the occipital and frontal slope steeper, while the temporal depth index is less, probably largely because the general length is larger. The stemangle was smaller than in the lower paleolithic or Neanderthal race.

The rostrum orbitale seems to be smaller in the Aurignac and Predmost races than in Neanderthalmen (cf. fig. 116 B and 119), but nevertheless it apparently is still well developed and also extends dorsally as well as ventrally to the lateral horizontal. The frontal lobes of the Predmost casts differ from most Neanderthal casts by being broader and more blunt at the ventro-frontal margin (fig. 120 A). On the Combe Capelle cast the impressions are not distinct but on the frontal lobes of the Predmost casts several fissures can be traced.

The ventral sulci are well expressed (fig. 120 B). The *frontalis inferior*, though its connection with the precentralis fails, is clearly indicated. In Predmost IV its ram. anterior is better developed than in any Neanderthal man, and in N°. IX it tends to connect with the midfrontal as often observed in recent men. In all casts the ram. inferior fiss. front. inf. is evident. In Predmost IX (right hem.) it ends in a distinct f. axialis operculi orbitalis. Between the *fronto-marginal fissure* (9) and the medial margin of the brain *convolutions* have developed *parallel* to the anterior margin of the frontal lobe as often observed in recent men. The *subfrontalis* is seen in all casts. In contrast to Neanderthal casts the impressions of *rami anteriores f. Sylvii* are very evident in all casts. In one (IX) there are clearly two rami, in another (IV) there may be a single ramus anterior. Moreover on three hemispheres a *fiss. axialis operculi frontalis* (a. o. f.) is indicated, on cast IX (right) even two.

In cast N°. III two symmetrical indentations before the lambda suture remind us of the same condition in the Rhodesian. That this has nothing to do with lunate sulci appears from the fact that on the left occipital lobe of the same brain a lunate sulcus is indicated on this cast, 1.1 cm. behind the lambda suture. The same is observed on the left occipital pole of Predmost X.
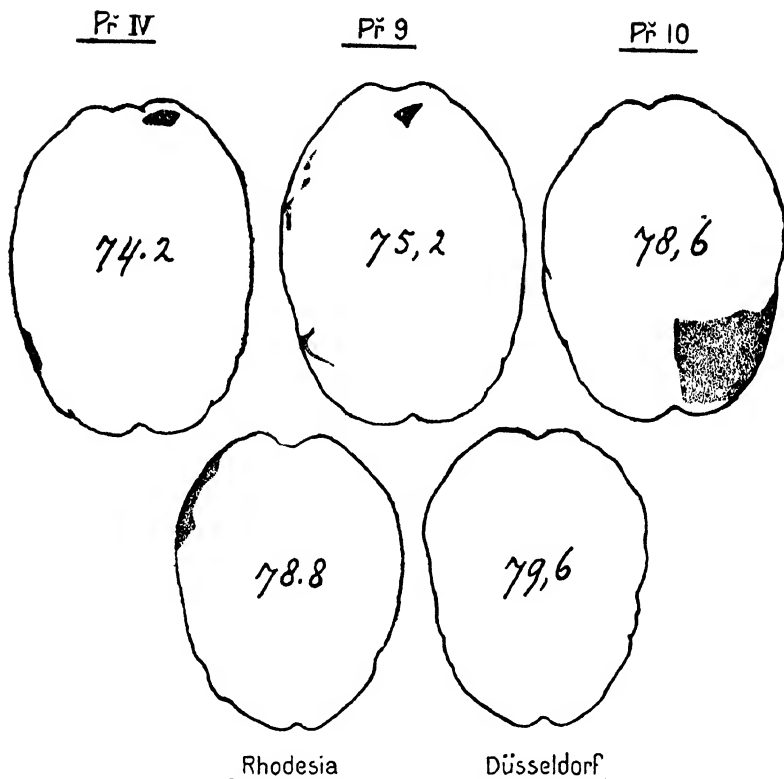
Fig. 120 A. Horizontal tracings of three upper paleolithic casts
(Pr. IV, IX and X) and two lower paleolithic casts.

So the endocranial features of this upper paleolithic race which generally is considered to be related to the CRO-MAGNON man do not reveal essential differences with present races and justify its name as Homo sapiens fossilis.

Much later in the epipaleolithic or mesolithic period a new race appears showing Azilian culture. About that period, preceding the neolithic area, several exquisite brachycephalic skulls occur in Europe. These are the skulls found by SCHMIDT near Nordlingen, (Ofnet) in Bavaria. The majority of the 20 skulls found there, were brachycephalic. The presence of these skulls at that place is probably due to the invasion from central Asia, the center of brachycephalic men and probably of Azilian culture (see the results of CHAPMAN ANDREWS expedition). I could not examine endocranial casts of these skulls, nor of the neolithic races, which probably differed little from recent races.

Fig. 120 B. Frontal fissures on the endocranial casts of Predmost III ♂, IV, IX and X.

Plate VII.

Semifrontal aspect of the endocranial cast of Predmost IV. Note the frontal extension (4ª) of the f. front. inferior and the fiss. axialis operculi (a. o.) in front of the ram. anterior ascendens fossae SYLVII (2ª).

EXPLANATION.

1 = fiss. sub frontalis.
2ª = ram. ant. ascend. f. SYLVII.
a. o. = fiss. axialis operculi.
4 = fiss. front. inferior.
4ª = ram. ant, f. front. inf.
4 i = ram. inf. f. front. inf.
4* = ram. ascend. f. front. inf.
4 ′ = fiss. front. infer. accessorius.
5 = fiss. praecentralis.
7 = fiss. frontalis medius.
7c = ram. connectens f. front med. et′ f. front. inf.
8 = intermediate fosset.
9 = fiss. fronto-margin.
11 = fiss. front. superior.
p = parellel convolution.

Plate VIII.

Approximately lateral aspect of the endocranial cast of Predmost N°. III ♂. Note the presence of a fiss. axialis operculi frontalis (a. o. f.) in front of 2, the anterior (ascending) branch of the fossa SYLVII.

EXPLANATION.

1 = f. subfront.
2 = ram. ant. (asc.) f. SYLVII.
3 = fiss. axialis operculi orbitalis.
a. o. f. = fiss. axialis operculi frontalis.
4 = fiss. front. infer.
4 i = ram. infer. fiss. front. infer.
4′ = fiss. front. inf. accessorius.
c = ram. connectens?
5? = f. praecentralis?
7 = fiss. front. med.
8 = intermediate fosset.
9 = f. fronto-marginalis.
9 p = ram. post. f. fronto-marg.
11 = fiss. front. superior.
p = parellel convolution.

RECENT RACES.

The Brain of a recent paleolithic race.

Most authors consider the Australian aboriginals as related to the Homo sapiens fossilis, without any genetic relationship with Neanderthalmen (BOULE, KLAATSCH, DUBOIS). Also the WADJAK proto-australian skull found on Java (DUBOIS [1])) has more upper paleolithic than Neanderthaloid characteristics.

It seems to be different with the fossil skull found at Tamworth in Australia, and described by BURKITT and HUNTER [2]), who emphatically call this hyperdolichocephalic skull (index 65) Neanderthaloid [3]).

That the present living Australian is more related to the North-western races than to the Asiatic and Indonesian Mongols, appears from their exquisite dolichencephaly and from the fact that in their serum the quality B, so characteristic of Mongols, is very scarce, while A. prevailing in Western races, is abundant. DOUGLAS LEE found the following reactions in 377 Australians of N. Queenland: O, 60.3%, A 31.7%, B 3.6 and AB 1.6%; CLELAND-BUSTON [4]) in South-Australians: O, 46%, A 54%, no B and no AB (101 individuals). TEBBUTS and Mc. CONNELL who examined 1176 pure Australians found O: 56.6%, A 36,9, B 8.5 and AB 2%. These figures are totally different from the Mongol and approach the Western races.

Whatever may be its relations, the recent Australian race, is a very primitive race somatically as well as culturally. Like the Neanderthalman of Europe it has none but lower palaeolithic implements, and produces no pottery nor artistic paintings and sculpture.

Its brain has been examined by MIKLUCHO-MACLAY [5]), ROLLESTON [6]),

---

[1]) DUBOIS. The protoaustralian fossil man of Wadjak. Proc. of the Kon. Akad. v. Wetensch., Amsterdam, Vol. 23, 1921.

[2]) BURKITT and HUNTER. Description of a Neanderthaloid australian skull with remarks on the production of the facial characteristics of australian skulls in general. Journ. of Anat. (Engl.) Vol. 57, 1922.

[3]) Also GRIFFITH TAYLOR (Environment and Race, Oxford Univ. Press. 1927) advocates a south-eastern migration of the bulk of this race.

[4]) Quoted from HIRSZFELD Constitutions serologiques (p. 100). For TEBBUTS and Mc. CONNELL see Medic. Journ. of Australia. Febr. 1922.

[5]) MIKLUCHO-MACLAY. On some peculiarities in the brain of the Australian aboriginal. (On a complete debouchement of the Sulcus Rolando into the fiss. Sylvii in some brains of Australian aboriginals). Proc. Linn. Soc. of New South Wales, Vol. IX, 1885.

[6]) ROLLESTON. Description of the cerebral hemispheres of an adult australian male. Journ. of the Anthr. Institute of Great Britain and Ireland, Vol. XVII, 1887.

MACALISTER [1]), FLASHMAN [2]), KARPLUS [3]), DUCKWORTH [4]), KOHL-BRUGGE [5]), WOOLLARD [6]) and myself.

HAUGER (l. c.), compared the endocranial capacity of twenty Australian skulls, described by KLAATSCH [7]), with European skulls. He found the average capacity to be 1146, being 311 cm.³ less than in the Europeans which he measured in the same way (cf. p. 206).

DAVIS and TURNER found the average capacity of 34 skulls 1230 cm³., and DUCKWORTH determined the average of 150 skulls to be 1246³. All these results [8]) point to a lower capacity than in Europeans of similar body size, and consequently to a lower cephalization coefficient.

DAVIS [9]), who estimated the weight of 17 ♂ and 7 ♀ Australian brains, found as (lowest, highest and) *middle weights*, in the former (1040, 1512 and) 1197 gr.; in the latter (968, 1249 and) 1123 gr. and concludes that the average of male and female is 1160 gr., about 11% less heavy than in the European. If we take the Pithecanthropus brain weight to be 970 gr. and that of the European to be 1300, the Australian (1160 gr.) holds the middle between them.

The brain of the related but extinct Tasmanian has been described

—————

[1]) MACALISTER. On the brain of the Australian. Proc. Brit. Ass. f. Adv. of Sciences 1892.

[2]) FLASHMAN. The evolution of the parieto-occipital fissure as demonstrated in some aboriginal brains. Reports from the pathological laboratory of the Lunacy Department, New S. Wales Government, Vol. 1, Part I, 1903; the same: Description of sulci of four brains of australian aborigines, ibidem Vol. I, Part I, 1903; the same: The morphology of the brain of the australian aboriginalI, bidem Vol. I, Part III, 1908; the same: The relation of brain to skull with special reference to the australian aboriginal, Ibidem Vol. III, 1916.

[3]) KARPLUS. Ueber ein Australiergehirn, nebst Bemerkungen über einige Negergehirne. Obersteiner's Arbeiten, Heft IX, 1903.

[4]) DUCKWORTH. On the brains of aboriginal natives of Australia in the Anatomy School, Cambridge; Journ. of Anat. and Physiol., Vol. 42, 1908. (three communications).

[5]) KOHLBRUGGE. Die Gehirnfurchen malayischer Völker verglichen mit denen der Australier und Europäer. Verhandl. Kon. Akad. v. Wetensch. D. 15, 1909.

[6]) WOOLLARD. The Australian aboriginal brain. Journ. of Anatomy (England) Vol. 63, 1929.

[7]) KLAATSCH. The skull of the Australian aboriginal. Reports from the pathological laboratory of the Lunacy department New S. Wales, Government Vol. I, Part III, 1908.

[8]) For quotations see KAPPERS. Proc. Kon. Akad. v. Wetensch. 1928.

[9]) DAVIS. Contributions towards determining the weight of the brain in different races of man. Phil. Transactions of the Royal soc. London Vol. 158, 1869.

by ELL. SMITH [1]), while that of the present living related aboriginal of New-Guinea, the Papua, has been described by BOLK [2]).

Finally VERMEULEN examined the Oblongata of two Melanesians (see below).

MANOUVRIER [3]) described a polynesian brain. This brachycephalic race is, however, not related to the above mentioned dolichencephalic races.

Of those authors who examined the morphology of the Australian brain special mention should be made of FLASHMAN, who first introduced standard lines for the callosum, among which the angle between the greatest length of the corpus callosum and the general direction of the spinal cord which he found to be 100° in an European woman (probably a brachycephalic) and 105° in his Australian. He also measured the slope of the longitudinal axis of the callosum to two basal skull lines, one running from the basion to the middle of the cella turcica, the other to the middle of the anterior fossa cranii. The callosum angle with the former line was 48,5° in his European and 50° in his Australian, with the latter line 24,5 in his European, and 26,5 in his Australian.

FLASHMAN further stated that the relation of the greatest length line of the callosum to the plane of the foramen magnum, gave 13° in the European and nearly 0° in the Australian, where these lines run almost parallel.

An interesting point is the caudal extent of the splenium callosi in regard to the perpendicular upon the middle of the basion-opisthion line. In his European the splenium fell short of this line by 1,3 c.M.; in his Australian, however, it passed beyond it by 0,5 c.M. Although Flashman only compared two brains, this was the first attempt to introduce standard lines and angles in brain anthropology, a necessity also expressed by HRDLICKA [4]).

Whether or not there is any relation between the Neanderthal and Australian races, or whether the brain of the latter shows a greater resemblance in its pattern with that of the upper paleolithic men this much is sure that, compared with European races, the Australian brain has some primitive features.

As such may be mentioned its prevailing dolichen- or mesencephaly, or rather the absence of pronounced brachencephaly, the small height of the calotte part and consequently the sloping frontal lobes, and occipital elongation, and perhaps also a somewhat greater stem angle.

[1]) ELL. SMITH. Le cerveau d'un Tasmanien. Bull. et mém. de la Soc. d'Anthrop. de Paris, Déc. 1911.

[2]) BOLK. Das Gehirn eines Papua von Neu-Guinea. Petrus Comper, Deel 3, 1905.

[3]) MANOUVRIER. Le cerveau d'un polynesien. Bull. Soc. d'Anthrop. de Paris, and Description d'un cerveau des îles marquises. Assoc. franç. de l'avancement des Sciences, 1892.

[4]) HRDLIÇKA. Anthropometry, Wistar Instit. Publ. 1920.
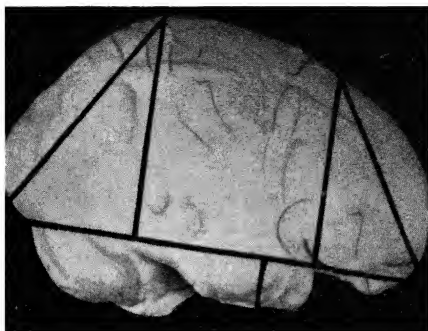
Fig. 121. Endocranial cast of an Australian
aboriginal's skull by ELL. SMITH.

Also the orbital keel is well pronounced in the Australian
as is the indentation of the ventral margin of the temporal lobe
by the petrosal bone (fig. 121; similarly in KEITH's cast.)

Furthermore in the brain described by KARPLUS the sulc. lunatus
is very pronounced on both sides [1]. FLASHMAN and WOOLLARD found
this sulcus more frequent and more strongly expressed in the
Australian than in the Europeans (also in ELL. SMITH's Tasmanian
it was quite distinct on the left side).

DUCKWORTH found the intraparietal deeper than the central
fsulcus as CUNNINGHAM observed in Anthropoids. DUCKWORTH further
called attention to the frequently more oblique course of the central
sulcus (fig. 122), correlated with the hyperdolichencephaly.

Comparing the frontal fissures of the Australians with those of
recent Europeans, I cannot omit saying that it seems to me that
the Australians show a certain simplicity. This is also expressed by
the fact related to me by Dr. WILKINSON of Sydney who said that
Australian anatomists rather demonstrate the frontal fissures in
aboriginals than in Europeans on account of their greater simplicity.

The sulc. frontalis medius (fiss. 6 and 7) is rather primitive
(DUCKWORTH, WOOLLARD) and shows Neanderthaloid relations in this
respect that 7 is connected with the precentral (5) by an arch (6)

---

[1] It seems well worth mentioning here that in an European imbecil, examined
by SANDER (Arch. für Psychiatrie, Bnd. V, 1875, p. 842) a sulcus is already
described as distinctly simian, specially on account of its opercularization.

which in higher brains mostly acquires a certain independency. In
fig. 122 III, IV and fig. 123 A and B there is a connection of 8 with
4 as in the Rhodesian cast. Further fissure 4—3 in brain II fig. 122
(right lobe) resembles the 4—3 relation in the Düsseldorf Neander-
thal man. In fig. 123 A and brain III fig. 122 (both right hemis-
pheres) there is only one anterior Sylvian branch (2). Similarly on
the left hemisphere in fig. 123 B. As this however also occurs in
Europeans in 41% on the right hemisphere (in 14% only on the left)
larger statistical figures concerning Australian brains are necessary.

I further want to call attention to the fact that in my Australian
(fig. 123 B) the anterior branch of the inferior frontal fails on the left.

Furthermore the subfrontal fissure (1), though occasionaly well pro-
nounced in Europeans seems more striking in the Australian although
it' is usually described as a part of the orbital fissures (fig. 123 B).
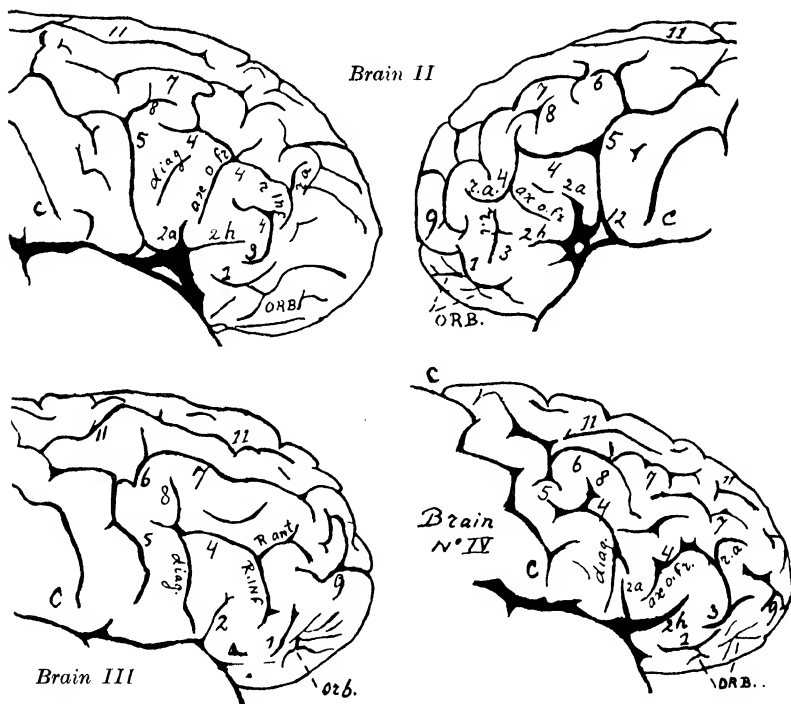
Fig. 122. Frontal fissuration in Australian aboriginals after Duckworth.
Same numeration of fissures as in fig. 119.

Fig. 123 *A*. Australian brains (III and IV of Flashman).

Fig. 123 *B*. Frontal and orbital fissures in an Australian brain
of my collection.

There are, however, characteristics hitherto not observed in paleolithic casts, e. g. the ventral elongation of the precentral fissure (5) as such or as a diagonal fissure (dia).

The sulcus axialis operculi frontalis (ax. o. fr., fig. 122) observed in the brains of DUCKWORTH fails in most other hemispheres represented here. As mentioned above this fissure is never seen on the Neanderthal casts, where also two anterior Sylvian branches cannot be stated beyond doubt. The latter, however, occur in upper paleolithic men where also a sulcus axialis operculi frontalis in frequently observed (see p. 243).

Although we should be careful with generalizing, it does not seem exagerated if we say that the Australian frontal lobe may be slightly simpler than the European.

In my Australian brain I am also struck by the rather blunt and turned inward form of the temporal lobe, (fig. 123 B), a characteristic not typical in European dolichocephalics and more obvious still in primitive brains.

WOOLLARD found the paracalcarine fissure more pronounced in Australians than in Europeans and frequently observed an exposed insula, but he found the same cortex percentage per hemisphere as in the European.

In his Papua brain BOLK was also struck by the simplicity of gyration and the large lateral extent of the parieto-occipital sulcus.

I finally want to mention that in two adult Melanesians VERMEULEN (l. c. infra) found the relative size of the spinal part of the hypoglossus nucleus larger and the bulbar (precalamic) part smaller than in Europeans, as also occurs in Hottentots (vide infra), and in wild animals compared with domesticated ones of the same order.

Negroid races.

Before dealing with the brain of present negroid races I have to mention two prehistoric negroid skeletons, the possessors of which were perhaps more or less contemporary with (BOULE), but certainly different from the Neanderthal men, and also from the Aurignac race. They lived before the latter, as appears from the fact that they were found at a depth of eight M. below a Cro-Magnon finding in the grotto's of Grimaldi. Similar skulls have been found in Switzerland, and in the North of Italy.

These *negroid skulls of Grimaldi* are hyperdolichocephalic (index

68 and 69), and higher than those of Neanderthal man. They also have a great cranial capacity (the adult 1580, the non-adult 1375 cm³). According to Boule (l. c. p. 274) we have to consider these people as belonging to the earliest reindeer period, the Aurignacian period, which followed immediately and may have been partly contemporary, in Europe at least, with the latest Neanderthal men. These negroid skeletons resemble those of the Bushmen-Hottentots.

By their short size (1,56 and 1,60 M.), the same sort of prognathism, platyrrhiny, length of face and dolichencephaly they specially resemble the "Hottentot Venus", from whom they differ only by the higher skull (Boule, l. c. 281).

The relationship between the South-African Bushman and Hottentots on the one hand and some early Aurignacian people of Europe on the other seems to be supported by the characteristics of the fossil skull found at Boskop in the Transvaal (index 75). This skull stands midway between the features of a reindeerman skull and that of a Bushman or Bantou (Boule l. c. 394).

Another argument for a relationship between some early inhabitants of Europe and the present living Bushmen-Hottentots is afforded by the steatopygy and the large labia minora (Hottentot apron) observed among the latter, which are also represented on sculptures of women found in Aurignacian deposits. Furthermore, the mural pictures of Bushman and Aurignacian races show a striking resemblance.

It may be that ancestors of the present Bushmen-Hottentots have lived in Spain and France in Aurignacian times, and were driven south by the later reindeer races, the Solutrean and Magdalenean people.

According to the latest researches of Pittard [1]) who examined the largest number of crania, the average capacity of the male Bushmen-Hottentots is 1395.3 ccm. [1]) (Broca found 1317 ccm.), in the female the average capacity is 1268.6 (Broca, 1253 ccm.), which would give a brainvolume of 1269ccm. for men and 1154 gr. for women and a weight of 1343 gr. for men and 1196 gr. for women. Marshall's Bushwoman's brain was reported to have a fresh weight of 30.75

---

[1]) Pittard. La capacité cranienne des Bushman-Hottentots. Co. rendus des séances de la Soc. de physique et d'histoire naturelle de Genève, 1927.

In the Griquas whom Pittard supposes to be related to the Bushmen-Hottentots, the average cranial capacity in the male is 1402 c.cm., in the female 1277,5 c.cm.
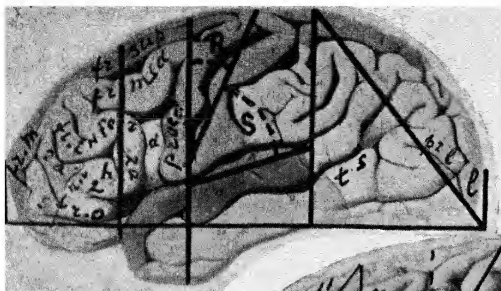
Fig. 124.
Brain of TIEDEMANNS
Hottentot Venus.

Fig. 125.
MARSHALLS Bush-
womans brain.

A
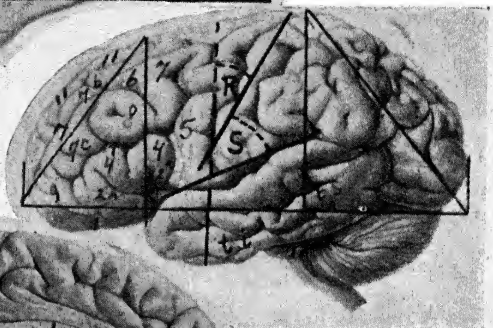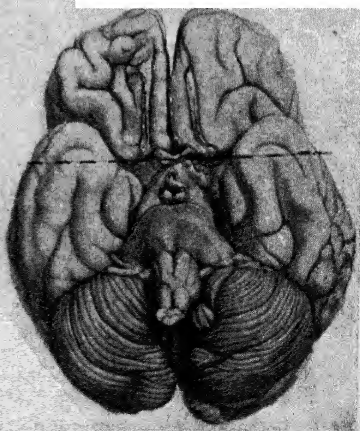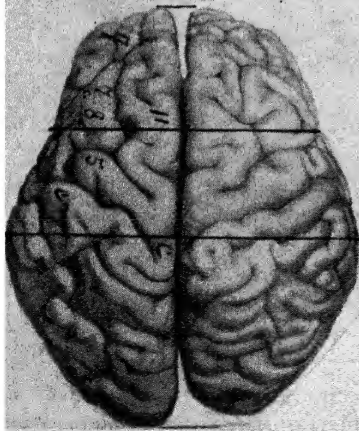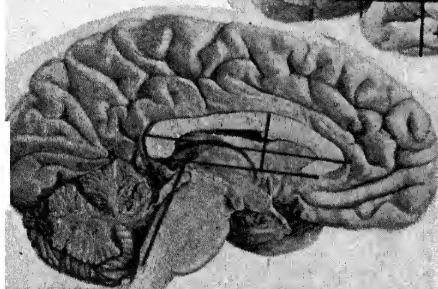
R. = Rolandic angle (mihi); S. = Sylvian angle (mihi);
l. = lunate; pr. l. = prelunate sulcus.

English ounces. KOCH's Bushwomans brain 28 German Unzen [1]).
SERGI's Hottentot brain weighed 1201 gr.

The external length width index of the male Bushman skull accord-
ing to R. MARTIN is 76.3 of the female 73.5 (WERNER [2])).

The brain of the present Hottentots-Bushmen has been described
by TIEDEMANN [3]), MARSHALL [4]), (fig. 124, 125), KOCH [5]) (fig. 126),
SERGI [6]), and RAWITZ [7]).

MARSHALL's Bushwoman's brain shows s simpler structure than
KOCH's though both are conspicuous by the narrow width of the
frontal lobes or rather pronounced parietal width (also characteristic
of negroes proper; see p. 260).

MARSHALL's brain shows a frontal and occipital flatness and relative
simplicity of its rather bulky convolutions. Measuring the indices
of TIEDEMANN's Hottentot brain (as reproduced by BISCHOFF) I
got very similar results to that of MARSHALL's Bushwoman (see the
list of indices on page 242).

KOCH, though stating the strong gyration of his brain, is struck
by the pronounced rostrum orbitale, a primitive feature. SERGI's
Hottentot brain seems about as richly convoluted as KOCH's
Bushwoman brain. It does not show primitive features, unless
one would consider as such an anastomosis of the ramus posterior

---

[1]) These weights (872 and 844 grs.) are too small. While KOCH's skull capacity
was 1085 cm³., the brain volume was probably no less than 976,5 c.cm., which
gives a weight of 1012 gr. PITTARD himself calculated an average female
brain weight of 1102.3 gr., an average male brain weight of 1177.6. In the
Cape colony the average weight of brains is given smaller: 1026.6.

[2]) PITTARD, to whom we owe the most recent figures found 64% of the males
to be dolichocephalic, 27% subdolichocephalic and 9% mesocephalic, while
of the female skulls 45% were dolicho- or subdolichocephalic, 25% meso-
cephalic and 30% subbrachycephalic or brachycephalic. Bull. et mém. de
la soc. d'Anthrop de Paris. Tome IX, 1928.

[3]) TIEDEMANN's „Hottentot Venus" brain is reproduced in BISCHOFFS
Grosshirnwindungen des Menschen. Abhandl. der Bayerischen Akad. der
Wissensch. Bnd. X, 1870.

[4]) MARSHALL. The brain of a Bushwoman. Phil. Transact. of the Roy. Soc.
London Vol. 104, 1864.

[5]) KOCH. Ueber das Gehirn eines Bushweibes. Inaug. Abhandl. Tübingen 1867.
(the figures are printed in LUSCHKA's Handb. der Anatomie).

[6]) SERGI. Osservazioni su due cervelli dit Ovambo ed uno di Ottentotta.
Atti della Soc. romana di Antropologia, Vol. 14, 1908.

[7]) RAWITZ. Bushmangehirn. Zeitschr. f. Anat. und Entw. Gesch. Bnd. 82,
1927 (obviously distorted material).

fossae Sylvii with the superior temporal, a feature also occasionally found by SERGI in Hereros.

Though none of the brains hitherto described show primitive features of the frontal convolutions, HENNEBERG found the relation
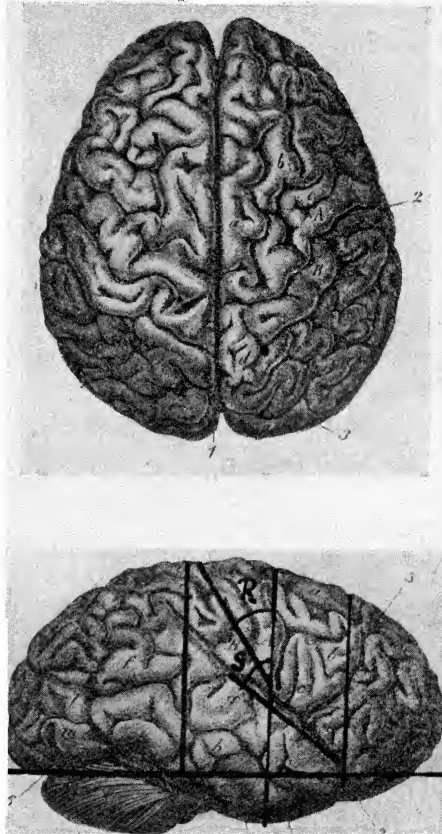
Fig. 126. Brain of Koch's Bushwoman.

of the frontal to the total cortex smaller in his Hottentot than in the European and Javanese he examined. He also found a smaller relation of the hidden cortex to the exposed one (cf. p. 264).

VERMEULEN found the relative size of the spinal part of the

hypoglossus nucleus in the Hottentot larger, the bulbar (precalamic) part smaller than in Europeans [1]), similarly as in Melanesians.

The origin of the *real negro races* of South Africa is unknown, but in some way or other they are related to the Bushmen-Hottentots [2]). The central african dwarfish negrillos especially seem to be closely related to the Bushmen (BOULE), with whom they share many somatic features, e. g., the dolichocephalic skull and small body.

Most negro brains that have been described are from Central- and Southwest Africa. From here also many American negroes originate. WALDEYER found the average brain weight of male Swahelis and Unyamwesis [3]) 1148 gr. but SANTON, HUNT and IRA RUSSELL found 1331 gr. for American negro soldiers (taller, selected men probably).

The latest figures concerning the weight of the American negro brain are those given by BENNETT BEAN [4]). They are taken from fresh material, and compared with fresh weights obtained by the same author in white Americans. On an average of 51 adult male negroes he found 1292 grams which agrees with the average of eleven adult male Herero's given by SERGI [5]) (1315 grams). BEAN found the average white male american brain 1341 grs. (Dutch males 1350 gr.), i.e. 49 grs. more than in his negroes. This difference agrees with the slightly smaller skull capacity of the male negro compared to the male white, as recently stated by WINGATE TODD [6]), who found a difference of 41 c.cm.

As, moreover, the average stature and body weight of the negro is a little larger than that of the american whites studied by TODD and LINDALA [7]) we may accept that the coefficient of cephalization in these negroes was slightly smaller than in the whites.

---

[1]) VERMEULEN, Influence of domestication on the structure of the brain. Proc. Kon. Akad. v, Wet, Amsterdam, Vol. 27, 1924.

[2]) Some ethnologists consider the Hottentots, as a mixture of Bushmen and equatorial negroes and add the Griquas to this group.

[3]) WALDEYER's material consisted of one Zulu, four Swaheli, two Sudanese, four Unyamwesi and one Ukarmi brain.

[4]) R. BENNETT BEAN. Some racial peculiarities of the negro brain. American Journ. of Anatomy, Vol. 5, 1906.

[5]) S. SERGI. Cerebra hererica. Denkschriften der mediz, naturw. Gesellsch. zu Jena, Vol. 15, 1909.

[6]) WINGATE TODD. Cranial capacity and linear dimensions in white and negro. Amer. Journ. of phys. Anthropology, Vol. 6, 1923.

[7]) WINGATE TODD and A. LINDALA Dimensions of the body; whites and American negroes of both sexes. Am. Journ. of Phys. Anthrop, Vol. 12, 1928.

For his study of the general morphology of the brain, as seen from above, BEAN used a horizontal circle, the diameter of which, drawn between the hemispheres had the length of the longitudinal axis of the brain.

This circle he divided in six equal sectors. For the study of the sagittal profile he drew the greatest longitudinal diameter passing on the mesial side underneath the splenium of the callosum and over the anterior commissure. This diameter runs through the foramen of Monro and the knee of the callosum. From the centre of this line he drew two radii at intervals of 60° and he measured the perpendiculars from the points where these radii pass the dorsal periphery of the brain to the sagittal diameter.

BEAN found that the negro brain seen from above is more blunt frontally than the brain of the white American. Laterally it is more flat than the white american brains used for comparison. Viewed from the side, the negro brain seems to be compressed caudally,
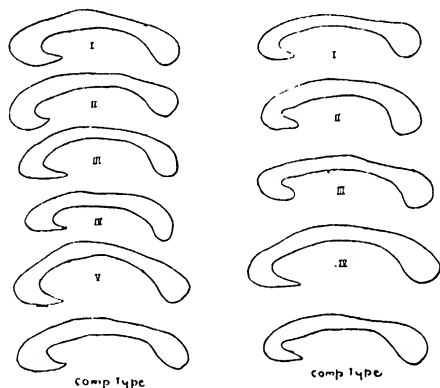
Fig. 127. Form of the corpus callosum in whites (left) and negroes (right) after BENNETT BEAN.

bulging in the parietal region, while the white's brain seems to be higher frontally; so that the frontal part of the brain of the negro seems smaller, the parietal larger (cf. also fig. 125 MARSHALL's Bushwoman) than in the white, a statement also made by POYNTER. BEAN corroborated this view by measuring the surface in front and behind the Rolandic fissure and the transverse surface of the callosum at the knee, body, isthmus and splenium.

While the area of the callosum varies with the brainweight, he found the anterior part of the callosum to be slightly smaller in the negro than in the white, which agrees with the smaller frontal lobe.

These interesting conclusions need further confirmation, though BEAN has checked his results as much as possible. It is a pity that he does not say to what white races the brains, used for comparison, belong. It may make a good deal of difference whether we compare the typically dolichencephalic negro (index 69,8—74,8; MARTIN [1])) with northern or mediterranean dolichencephalics or with alpine brachencephalics, as the indices influence such comparisons, and even the form of the callosum (see p. 279).

The convolutions of the negro brain have not been described by BEAN. Descriptions of them are given by TIEDEMANN [2]), PARKER [3]), WALDEYER [4]), ELL. SMITH [5]), SERGI [6]), POYNTER [7]) and GENNA [8]). Leaving aside the older tendentious literature on this subject, which has been justly criticized by KARPLUS (l. c. supra), WILDER [9]) and MALL [10]), I shall mention only some of the conclusions reached by WALDEYER, ELL. SMITH, SERGI, GENNA, and POYNTER.

---

[1]) MARTIN. Lehrbuch der Anthropologie, Fischer, Jena, 1914.

[2]) TIEDEMANN. Das Gehirn des Negers mit dem des Europäers und Orang Utan verglichen. Heidelberg 1837 (also published in the Transactions of the Roy. Society, London. Vol. 126, 1836).

[3]) PARKER. The cerebral convolutions of the negro. Proceed. of the Philadelphia Academy of Natural Sciences, 1878.

[4]) WALDEYER. Ueber einige anthropologisch bemerkbare Befunde an Negergehirne. Sitz. ber. der Preuss. Akademie der Wissenschaft, Berlin, 1894 and: Das Gehirn südwest afrikanischer Völker, ibidem, 1906.

[5]) ELL. SMITH. Records of the Egyptian school of medicine, Vol. II, 1904.

[6]) SERGI. Due cervelli di Sudanesi. Alli della Soc. romana di Antropologia Vol. XIV, fasc. III, 1908; Un cervello di un indigeno di Tabora (Unyanyembe), ibidem; Contributo allo studio del lobo frontale e parietale nelle razze umane, Osservazioni sul cervello degli Herero. Ricerche fatte nel laboratorio di anatomia normale di Roma etc. Vol. 14, 1908; Cerebra hererica, Denkschriften der mediz. naturw. Gesellsch. zu Jena, Vol. 15, 1909; Sui solchi temporo-occipitali inferiori nel cervello dell' uomo, Rivista di Antropologia Vol. 16, fax. I, 1911; Sulle variazioni dei solchi del lobo frontale negli Hominidae, ibidem, Vol. 18, fasc. I—II, 1913; Ueber die Morphologie und Symmetrie des lobus frontalis beim Menschen, Zeitschr. f. Morph. und Anthrop., Bnd. 17, 1926.

[7]) POYNTER. Some conclusions based on studies in cerebral Anthropology. The American Anthropologist, Vol. 19, 1917.

[8]) GENNA. Sulla morfologia dei solchi cerebrali dell Uomo con osservazioni su cervelli di indigeni del Camerum. Rivista di Antropologia, Vol. 26, 1924—1925.

[1]) WILDER. The brain of the American negro. Proceed. of the First National Negro conference, New York, 1909.

[2]) MALL. On several anatomical characteristics of the human brain said to vary according to race, sex, etc. American Journ. of Anatomy, Vol. 9, 1909.

WALDEYER (1906) called attention to the large "Olfactoriuswulst" in Herero brains, our rostrum orbitale, so striking in prehistoric brains. Fig. 128 shows it in a Sudanese examined by SERGI.

WALDEYER also mentioned a rather round temporal pole which thus covers the uncus hippocampi more completely than it does in Europeans and which he therefore called "Uncus deckel", or *operculum unci*.

KLASS [1]) recently compared the olfactory tracts in Europeans,
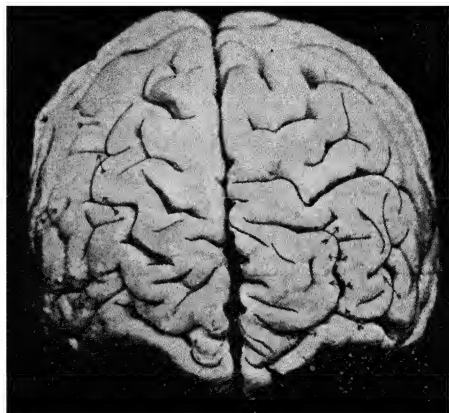
Fig. 128. Brain of a Sudanese woman, after SERGI.
Note the large rostrum.

Bantounegroes and Bushnegroids, but found in all of them the same variations.

In his painstaking work on the Herero brain SERGI comes to the conclusion that convolutional differences between Hereros and Europeans are small, even smaller than the convolutional differences between male and female representatives of each race in itself. — Moreover, these differences (as the sexual ones) are a question of frequency. Now we know that frequency figures of variations may change considerably with the number of cases examined. A variation in favor of one race may appear to be even more frequent in the other if a much greater number of brains is examined. Still this is the only way available at present in this kind of study, and I may not omit to mention the points in which a serious worker as SERGI

[1]) Journ. of Comp. Neur. 1929.

found frequency differences between his thirteen Herero's and his Europeans. (Germans? or Italians?).

SERGI confirms the pronunced development of the convolutions bordering the rhinal sulcus (WALDEYER's Olfactoriuswulst, our rostrum) which may also explain[1]) the pronounced rhinal sulcus found by ELL. SMITH. He also confirms the greater overlapping of the uncus by the blunt temporal lobe ("Uncusdeckel" of WALDEYER), and further mentions a constant occurrence of a rhinencephalo-temporal bridging convolution, and a more frequent continuation of the central sulcus on the mesial wall than in the European.

While the superior and inferior frontal sulci are more often represented by small non continuous fissurettes, he found the *s. frontalis medius more frequently continuous than in Europeans.* On the other hand he found the intraparietal sulcus more often divided into its three components, and a less frequent interruption of the superior temporal, and of the fiss. temporalis medius ($=$ inferior). Some of these features I also observed in paleolithic brains, e. g., the strong rostrum, the blunt temporal lobe and the continuous frontalis medius (see p. 232—234). It is interesting that, while WALDEYER found the horizontal anterior branch frequently failing, GENNA in eleven Cameron negroes found both rami anteriores fossae Sylvii "prevalentamente disposta ad Y" (l. c. p. 133) and the diagonal sulcus mostly absent or confluent with the precentralis inferior.

WALDEYER mentioned the large size of the cerebellum without, however, giving dhe cerebellar percentage, which may vary in all the races I examined from 8%—12% of the total brainweight.

In the North-American negroes (rarely pure from a racial standpoint), POYNTER found the frontal part of the brain less developed in comparison to the parietal (cf. BENNET BEAN). He found the fiss. frontomesialis[2]) remarkably constant (contrary to CUNNINGHAM l.c. p. 269), the s. frontalis medius[3]) poorly developed, and a long posterior calcarine sulcus.

[1]) The protrusion of the rostrum is not only confined to the gyrus rectus but may also imply the frontal part of the convolution lateral to the olfactory sulcus and so makes this sulcus (generally called s. olfactorius) deeper.

[2]) The fronto-mesialis (CUNNINGHAM) is a system of discontinuous fissurets between the S. frontalis superior and the mesial edge of the hemisphere.

[3]) This statement seems contradictory to SERGI's. As, however, POYNTER does not give pictures it may be that he alludes to another sulcus than EBERSTALLERS frontalis medius, there being a great deal of misunderstanding about what sulcus or system of fissurets should be called frontalis

Emphasizing the large size of the parietal lobe as BENNET BEAN did, he mentions the great amount of variation in the inferior parietal region, which, however, was also striking in the fifty Dutch brains examined by Dr. WANG HWEI WEN and me [1]). We found that the number of so called ascending branches of the superior temporal sulcus, the ascending branch proper, the s. angularis and s. occipitalis anterior of ELL. SMITH (SHELLSHEAR), may vary from one to three, the first one, the ascending temporal proper (also occurring in anthropoids), being the most constant, the second one, s. angularis (occurring also occasionally in anthropoids), less so and the s. occipitalis ant. least constant.

The amount of cortex in the Hottentot and Herero brain, in comparison to other races, may be calculated from HENNEBERG's [2]) figures concerning the surface extent of the left hemisphere, if we assume an equal surface on the right and an equal average depth of the cortex of about 2,5 mm. with a specific weight of 1,034.

R a c e.	Total brain weight.	weight hem. left	surface left hem.	cortex weight left hem.	cortex perc. per left hem [3]).	cortex perc. per total brain weight.	relation of frontal to total cort.
Europ. I ...	—	525 gr.	1082 cM.²	279,5 gr.	53,4 pCt.		1 : 1,97
Europ. II ..	1510 gr.	655 gr.	1240 ,,	320,5 gr.	48,9 ,,	42,2	1 : 1,98
Europ. III .	1320 gr.	565 gr.	1016 ,,	262,5 gr.	36,5 ,,	40.0	1 : 1,79
Hottentot ..	—	615 gr.	1119 ,,	289 gr.	47 ,,	—	1 : 1,67
Herero	1215 gr.	530 gr.	996 ,,	257,5 gr.	48,6 ,,	42,4	1 : 1,95
Javanese ...	1230 gr.	535 gr.	1050 ,,	271,5 gr.	50,7 ,,	44,9	1 : 1,78

From this appears that no important difference in cortex percentage per total brainweight exists. Whether there is a difference of cortex-weight percentage on bodyweight is not sure as HENNEBERG gives

medius. It seems best, as I did with may prehistoric casts, to stick to EBERSTALLER's interpretation, since he was the first to describe this fissure. Underneath it lie what I have called „intermediate" fissurets (see also Addenda).

[1]) WANG HWEI WEN and ARIËNS KAPPERS. Some features of the parietal and temporal lobes of the human brain and their morphological significance. China medical Journal, Sept. 1924.

[2]) HENNEBERG. Messung der Flächenausdehnung der Grosshirnrinde. Journ. f. Psychologie u. Neurologie, Bnd. 17, 1910—1911.

[3]) As I pointed out elsewhere (1925) the cortex percentage expressed on the hemispheres alone is not a trustworthy indicator of higher development as (with equal thickness of cortex) this percentage is necessarily higher in smaller brains. So Dr. A. TAFT found the cortex percentage in a tranverse section of the brain on the level of the optic chiasma to be greater in microcephalic idiots than in normal men. (Journ. of nerv. and ment. disease, Vol. 47, 1918.

no body weight figures. He did however find *a difference in the relation between the exposed cortex and the one hidden in fissures.* In his Herero and especially in his Hottentot the hidden cortex was less in relation to the exposed cortex than in his European and Javanese. HENNEBERG also found the relation of the frontal to the total cortex smaller in the Hottentot (not in his Herero). These interesting results should be controlled on more brains.
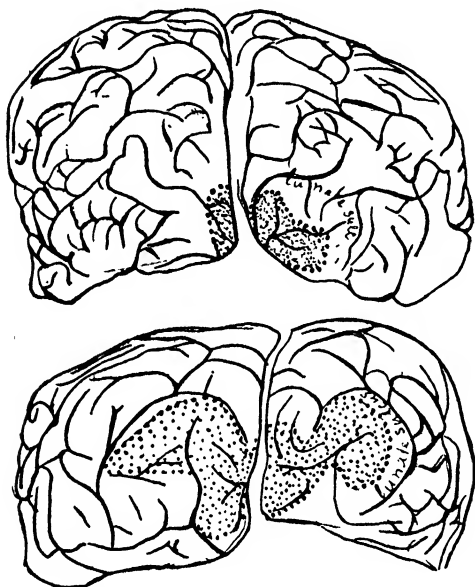
Fig. 129. Extent of the area striata in the brain of a European (top figure) and Herero, after BRODMANN.

Also some cytotectonic work has been done on negroes. BRODMANN [1]) found that in some African aboriginals he examined the striate area extends further lateral than is usually seen in Europeans.

He calculated the average surface of the striate area to be 2,78% of the whole surface of the cortex in five Europeans; in four Africans 2,81%. In the average European 9,8% of this field lies on the convexity; in the Africans he examined 27,1% (see fig. 129).

While the supposed relatives of the early Aurignacian negroids of Europe may now be confined to Southern and Central Africa, the

---

[1]) BRODMANN. Vorkommen der Affenspalte bei verschiedenen Menschenrassen. Archiv. f. Psychiatrie, Bnd. 48, 1909; and: Neue Forschungsergebnisse der Grosshirnrindenanatomie mit besonderer Berücksichtigung anthropologischer Fragen. Verhandl. der Gesellsch. Deutscher Naturforscher und Aerzte, 1913.

later, Solutrean and Magdalenean races of Southern Europe may survive in the Basques, in the Canary island Guanchees and North African population such as the Kabyles and Berbers (BOULE), perhaps also in the Egyptian Fellahs and Aethiopians or Abessynians.

Also the more slender human figures portrayed in Magdalenean times are more like the bodies of these peoples, than of the Bushman-Hottentot race. Steatopygy does not occur in Magdalenean pictures, nor in the above mentioned recent races.

The brain of the *Fellahs* is described by BENEDIKT [1]) and especially by ELL. SMITH [2]) who used this race, and the Sudanese, for his fundamental studies on the occipital lobe. In this important work he was the first to emphasize the very frequent occurrence of the *lunate sulcus*, the larger extension of the striate area on the convexity among this people and the occasional occurrence of the *limbus postorbitalis* [3]), a transverse orbital ridge in front of the insula. This ridge caused by the sphenoid bone was first described by SPITZKA [4]) in Papuas and Japanese, but it also occurs in Europeans, and more frequently even in the Chinese (KAPPERS). ELL. SMITH described also some disseccated early historic or prehistoric Fellahbrains (see p. 221).

The brain of a *Berber* has been described by LEGGE [5]), whose work was not accessible to me. Of an *Abessynian* brain we have a description by SERGI [6]), while COLE [7]) described the brain of an *Arab*. More researches on these races are necessary.

---

[1]) BENEDIKT. Ein Fellahgehirn. Mitteil. der Anthr. Gesellsch. Wien, Vol. 23, 1893.

[2]) ELL. SMITH. Studies in the morphology of the human brain with special reference to that of the Egyptians No. I. The occipital region. Records of the Egyptian Government School of Medicine Vol. II, 1904. See also: The morphology of the occipital region of the cerebral hemisphere in man and apes; Anat. Anzeiger Bnd. 24, 1904, and: The persistence in the human brain of certain features usually supposed to be distinctive of apes, Reports of the British association for the advancement of science, Cambridge, 1904 and: The so called „Affenspalte" in the human (Egyptian) brain. Anat. Anz. Bnd. 24, 1904.

[3]) ELL. SMITH. The limbus postorbitalis in the Egyptian brain. Anat. Anzeiger Bnd. 24, 1903.

[4]) SPITZKA. The postorbital limbus, a formation occasionally met with in the human brain. Philadelphia Med. Journ. April 1903.

[5]) LEGGE. Il cervello d'una berbera. Bolletini Lancisiani degli Ospedali di Roma, Fasc. 3, 1884, quoted from SPITZKA. Journ. of Anat., Vol. 2, 1902.

[6]) SERGI. Un Cervello d'Abissino. Archivio antropologico, Tomo 18, 1913.

[7]) Journ. of Anatomy and Physiology, Vol. 54, 1920.

Eskimo- and North-American Indian brains.

While all the races hitherto mentioned have found their refuge largely south of the Mediterranean, it is accepted by several authors that the prehistoric *Chancelade man,* contemporary with the European reindeer man may have migrated or returned to arctic regions with the retreat of the reindeer and the glaciers to these regions. TESTUT, DAWKINS, NERVÉ, SOLLAS, TAYLOR emphasize his similarity with the present living Eskimo, whose skull, as that of the Chancelade man, is conspicuous by its dolichocephaly (man 70.67, women 72.21; FÜRST and HANSEN l. c. infra), great height (width-height index 102.78, FÜRST and HANSEN l. c. infra), sagittal crest, and large capacity, combined with a small body size.

KEITH [1]), however emphatically denies a relationship between the Chancelade and Eskimo skulls.

Similarly it is supposed that the Canadian Algonquins and other North-American Indians are related to contemporaries of the Chancelade man, as the implements of the Algonquins are of the same character (SOLLAS) as those found near Chancelade.

This theory is supported by TAYLOR (l. c.) who believes that the Eskimos and the Canadian Algonquins belong to the same migration zone. Serology also points to a relationsship of the Eskimo and the North-American Indians; their blood constituents (see below) being very much the same.

Whatever may be his relations, the skull capacity of the Eskimo is about the same as that of the Chancelade man, both being large. The capacity of the latter is 1530 ccm. (LEE and PEARSON). For the Eskimo BROCA [2]) found this to be 1585 ccm. in the male and 1429 ccm. in the female; HRDLIÇKA [2]) 1563 in the male, 1458 in the female; FÜRST and HANSEN [3]) 1526 and 1435 c.cm. respectively.

Eskimo brains are described by CHUDZINSKI [4]), HRDLICKA [5]) and SPITZKA [6]).

---

[1]) KEITH. Was the Chancelade man akin to the Eskimo ? Man, Dec. 1925.

[2]) Quoted from MARTIN's Anthropologie.

[3]) FÜRST und HANSEN. Crania groenlandica, Höst, Copenhagen, 1915.

[4]) CHUDZINSKI. Les trois encéphales des Esquimaux morts de la variole. Bull. de la Soc. d'Anthr. de Paris, 1881. There are no figures in this paper.

[5]) HRDLICKA. An Eskimo brain. Proceedings of the Am. Med. Psych. Assoc. N. Y. 1899, and American Anthropologist, 1901.

[6]) SPITZKA. Contributions to the encephalic anatomy of races: Three Eskimo-brains from Smith sound. Am. Journ. of Anat. Vol. 3, 1902.

The size of the brain had already struck CHUDZINSKI, whose material, however, was not well enough preserved for other studies.

As far as concerns their dolichencephaly it seems that this is largely due to an occipital elongation, as is also the case with many fossil brains.

The frontal part is not sloping but steep, as appears from HRDLICKA's (fig. 130 B) and SPITZKA's figures, and from an endocranial cast (fig. 130 A) in my possession. The same is found with the Chancelade skull.

The rostrum orbitale [1]) is fairly pronounced. The fissuration is rich, not simpler than in Caucasian races and the convolutions are not bulky and are often divided by transverse fissures. SPITZKA rightly remarked that their tendency to numerous transverse anastomoses, frequently causing the interruption of some of the longitudinal fissures, is the more striking since this does not generally occur as much with pronounced dolichencephaly as with brachencephaly (CALORI [2]), MEYER [3]), RÜDINGER [4])).

SPITZKA and HRDLICKA's figures also show a lunate sulcus (cf. fig. 130 B) which, however, is rather frequent ($\pm$ in 25%) in all races.

The *North American Indians* were formerly considered by many authors to be mongoloid types on account of their somatic qualities [5]), but CLARE and VERZAR have pointed out that serologically they hardly have any B component which is so characteristic of the Mongols, while their A component is also extremely small, the large majority being *O*. If *O* is to be conceived as a peculiar blood quality, they have to be considered with the Eskimos as a race of their own.

The skull capacity of the North-American Indians is, however, smaller than that of the Eskimo. According to HRDLIÇKA (quoted

---

[1]) SPITZKA says (p. 49, 60): the mesorbital gyre is unusually narrow. The rostrum form is visible on his fig. 1, 5, 7, 11.

[2]) CALORI. Del cervello nei due tipi brachicefalo e dolicocefalo italiani. Memorie dell' Accademia delle Scienze dell' instituto di Belogna, Seconda serie, Vol. 10, 1870.

[3]) MEYER. Ueber den Einflusz der Schädelform auf die Richtung der Groszhirnwindungen. Zentralblatt f. die Mediz. Wissensch. Jahrg. 14, 1876.

[4]) RÜDINGER. Gehirnwindungen bei Lang- und Kurzköpfen. Korr.blatt der Deutsch. Ges. f. Anthr. 1877.

[5]) For a resumé of some opinions concerning their origin I refer to COTTE-VIEILLE-GIRANDET's paper in the Mém. de l'Inst. International d'Anthropologie, Session III, Amsterdam, 1928.
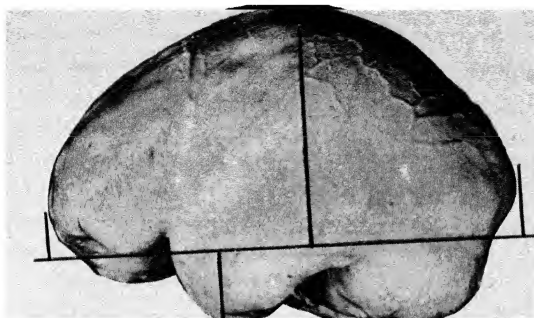
Fig. 130 A. Endocranial cast of an Eskimo
skull. Note the large rostrum.
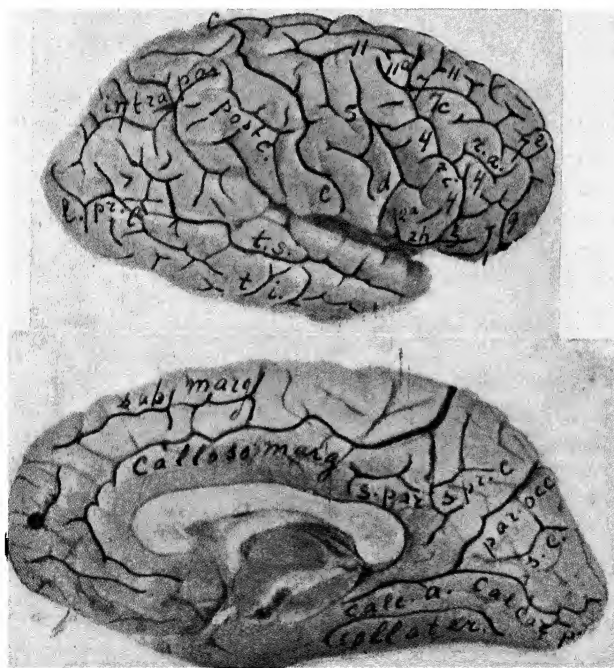
Fig. 130 B. Right hemisphere of the Eskimo brain described
by HRDLICKA. The lower photo is slightly less reduced than
the upper one. l. = lunate sulcus; pr.l. prelunate sulcus
connecting with the superior and inferior temporal.

from MARTIN) it is 1455 in the male Arkansas Indian, 1255 in the female. In the Araucanians DE QUATREFAGES found the difference between the sexes not quite so great (1420 and 1340).

According to KEEGAN [1]), only five brains of pure North-American Indians are preserved in American museums. Of these four are described by this author, a plains Indian brain, one of a full-blood Teton Sioux, two of full-blood Tonto-Apaches (apparently not well preserved).

He found no difference in comparison with the average white's brain, nor a close approach to the brain of the Eskimo or the Chinese. In some he found, as a primitive feature, a rather lateral extent of the postcalcarine fissure (though not as large as in the negroes he examined) and a fetal form of the rhinal sulcus.

Of the *South- and Central-American Indians* brain descriptions are given by FALLOT [2]), SEITZ [3]), MANOUVRIER [4]), BENEDIKT [5]), DANA [6]), JAKOB [7]) and POYNTER [8]).

Most of these descriptions are, however, founded on distorted material. In fig. 131 I give a photograph of a well preserved brain of an Indian from the North-coast of South-America in my collection. In this brain the Sylvian angle is rather small. Similarly the inclination angle between the Rolandic and Sylvian. There was a slight indication of a postorbital limbus, a small but distinct opening of the insula (which in a similar way also occurs occasionally in European material), a pronounced lunate sulcus, connected by a prelunate sulcus with the superior temporal fissure. The temporal lobe is strongly turned inward, and its pole is rather blunt.

---

[1]) KEEGAN. A plains Indian brain. Journ. of Compt. Neurol. Vol. 26, 1916 and The Indian brain, American Journ. of Physic. Anthropology, Vol. III, 1920.

[2]) FALLOT. Sur le cerveau d'une jeune indienne, née à Caracas. Bull. de la Soc. d'Anthrop. de Paris, 1880.

[3]) SEITZ. Zwei Feuerländergehirne. Zeitschr. f. Ethnol., Berlin, 1886.

[4]) MANOUVRIER. Le cerveau d'un Fuégien. Bull. de la Soc. d'Anthrop. de Paris, 1894 ser. IV, T. 5.

[5]) BENEDIKT. Ein Indianergehirn. Mediz. Jahrb. Wien H. F. Bnd. III, 1888.

[6]) DANA. The brain of a full-blooded Bolivian. Indian Journal of Nerv. and ment. dis. 1894.

[7]) CHR. JAKOB. Contribution à l'étude de la morphologie des cerveaux des indiens. Revista del Museo de la Plata, Tome XII, 1904.

[8]) POYNTER gives six aspects of a brachencephalic male mexican brain (index 85) in the American Anthropologist. Vol. 19, 1917.

I need not say that I am not inclined to consider these features as racial distinctions.

Asiatic Brains.

The brains of the inhabitants of the non-mongolian South-western part of Asia have been very rarely studied. Concerning the inhabitants of British
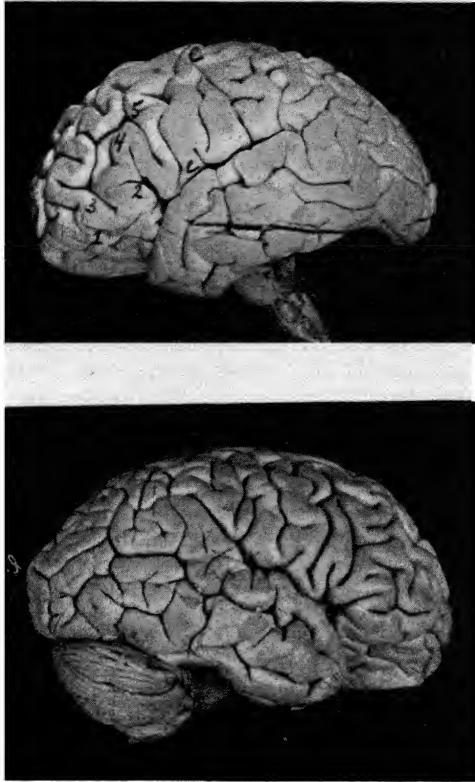
Fig. 131. Brain of a South American Indian.

India, we only have APPLETON's [1]) description of a Madrassi Hindu and a Tamil brain, SERGI's descriptions of the brains of two Tamils, one Hindu, one Faradula and four Laskares, and a note concerning an Arab and Goanese

[1]) APPLETON. Descriptions of two brains of natives of India. Journ. of Anat. and Phys. Vol. 45, 1911.

brain by Cole [2]). The brain of the interesting dwarfish dolichencephalic Weddahs of Ceylon has never been described, but Spitzka [3]) gave a short description of the brains of an Andamanese and Nicobar islander, for which I refer to the original. Appleton came to the conclusion that his Hindu and Tamil brain could not be distinguished from European specimens.

The great Mongolian group is usually divided into two branches: the central or northern Mongols, and the Tibeto-Indo-Chinese. To the first belong several groups, some of which inhabit northern Asia, and part of northern Europe, viz. the Lapps and Finns, forming the finnish-ugrian group to which also belong several inhabitants of Estonia and Lettland (Birkner) [4]).

The brain of the Esths, according to Weinberg [5]), offers some characteristics among which a more frequent anastomosis of the inferior praecentral and Sylvian sulcus than in other Europeans, but Landau [6]) and Gorgianoff [7]), obtained a practically negative result, as far as concerns distinctions with the general European type. Whatever may be the case, the figures published by these authors certainly do not reveal any mongol characteristics as e. g., the brain of the Lapp, decribed by Retzius, does (see p. 269). It is, however, remarkable that in the Letts Weinberg frequently found a hooklike calcarine as Mrs van Bork found in the Chinese (see fig. 136).

Also the Turks and Tatars (see fig. 132) proper are considered as an (impure) branch of the central Mongols.

The purest groups of the Central or Northern Mongols are the Kalmuks, Buriates, Samoyedes, Tonguse, Gobi-Mongols and Manchus.

---

[1]) Sergi. Note morfologiche sulla superficie metopica del lobo frontale in cervelli di indiani e di giaponesi. Richerche fathe nel laboratorio di anchonia normale della R. Universita di Roma etc. Vol. 17, 1913.

[2]) Cole. Fissural pattern in four asiatic brains. Journ. of Anat. and Physiology Vol. 54, 1920.

[3]) Spitzka. Preliminary note on the brains of natives of the Andaman and Nicobar islands. Proc. American Philosophical Society. Vol. 47, 1908.

[4]) Birkner. Die Rassen und Völker der Menschheit. Bnd. 2, Allg. Verlagsgesellschaft, Berlin, München und Wien.

[5]) Weinberg. Die Gehirne der Esten, Letten und Polen verglichen mit den Gehirnformen einiger anderen Völkerschaften. Compte rendu du XIIième Congres intern. de medicine, Moscow 1898.

[6]) Landau. Ueber die Orbitalfurchen der Esten. Zeitschr. f. Morph. und Anthrop. Band 12, 1909; Ueber die Furchen an der Medialfläche des Grosshirns bei den Esten. Ibidem Bnd. 13, 1910; Ueber die Grosshirnfurchen am basalen Teile des Tempero-occipitalen Feldes bei den Esten, Ibidem Bnd. 13, 1911; Ueber die Furchen an der Lateralfläche bei den Esten. Ibidem Bnd. 16, 1913.

[7]) Gorgianoff. Die Insula Reillii der Esten. Ibidem.

They are distinguished from the Tibeto-Chinese by being *brachy-cephalic*, whereas brachycephaly is an exception with the Chinese, who as a rule are mesocephalic.

KEANE [2]) gives the northern Mongols a length-width index of 84 and the Chinese an index of 77,25, while the index of the latter, stated by KOGANEI [3]) is 78,3, by HABERER [4]) 78,8 by REICHER [5]) 78,5.

It is important to mention these figures since KURZ (l. c. infra) calls the Chinese brachycephalic and compares their brain with that of the most brachy-cephalic anthropoid, the Orang Outan.

Besides, the Chinese are exquisitely hypsicephalic while the central Mongols are *platycephalic*; MOCHI [5]) and REICHER [6]).

The width-height index in Buriates is 85,9, in Kalmuks 87,5, according to REICHER (according to IWAN 88,7) while in northern Chinese it is 97,7, according to REICHER (100,2 after KOGANEI) and in the Formosa Chinese (KOGANEI) even 101,2. According to BLACK [7]) the prehistoric Kansu race was also meso- and hypsicephalic. As at that time the mixtures with other races, so emphasized by LEGENDRE [8]) probably were very rare, this seems to confirm the general conception (contested by LEGENDRE) that the Tibeto-Chinese group has its own characteristics.

To these general morphological differences in the skulls, some differences of the brain correspond.

In fig. 132 I give a photograph of a male Tatar brain from the neighbourhood of Kasan. This brain is brachencephalic and rather

---

[1]) The description of the brain of the Turks, and Georgians given by STEFKO in the Journ. russe d'Anthropologie, Tome 13, 1924 was not available to me.

[2]) KEANE, Ethnology. Cambridge Geographical Series.

[3]) KOGANEI: Messungen an männlichen Chinesenschädeln. Centralblatt für Anthrop. Bnd. 7, p. 129, 1902.

KOGANEI: Messungen an Chinesischen Soldaten. Mitteilungen der mediz. Fakultät der Kaiserl. japan. Universität in Tokyo, Bnd. VI, Heft 2, 1903.

[4]) HABERER. Schädel- und Skelettteile aus Peking. Ein Beitrag zur somatischen Ethnologie der Mongolen. Bnd. I, Gustav Fischer, Jena 1902.

[5]) REICHER. Untersuchungen über die Schädelform der alpenländischen und mongolischen Brachycephalen, Zeitschr. für Morph. und Anthrop. Band 15 und 16, 1913, p. 59 and 62.

[6]) MOCHI. Crani cinesi e giapponesi; Arch. per l'Anthropologia. Vol. 38, 1908.

[7]) BLACK. A note on the physical characters of the prehistoric Kansu race. Memoirs of the geological Survey of China. Ser. A. No. 5, 1925.

[8]) LEGENDRE. Il n'y a pas de race jaune. Mémoires de l'Institut internationale d'Anthropologie, Session III, Amsterdam 1928.

flat. It had the large weight of 1570 gr. GUILTCHENKO gives the
Tatars an average of 1386 gr., which — if it includes both men
and women — is also very high.

The two endocranial casts of Tatars in the Collection of the Royal
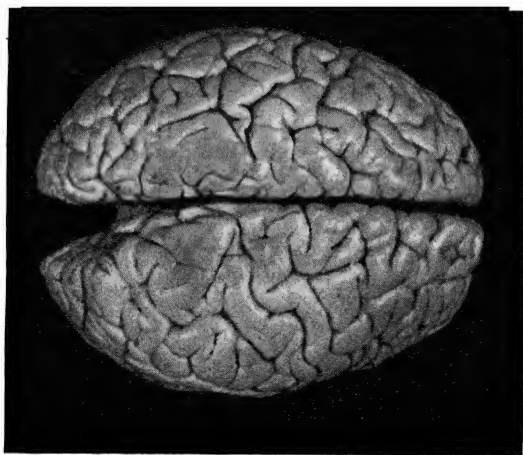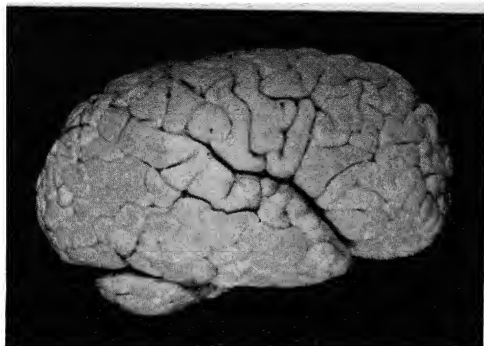
Fig. 132. Brain of a Tatar. The Sylvian fis-
sure, that was tightly closed is artificially
broadened to show clearer in the photo.

College of Surgeons, London, are nearly circular in the horizontal
plane, according to BURNE and ELL. SMITH's catalogue (D. 697).

BUSHMAKIN [1]), who recently described the brain of thirty five *Buriates* found the average weight (with pia and ventricular fluid) in males 1508 gr. (one male had a weight of 1934 gr.!) in females 1439 gr. TALKO HRYNTZEWITSZ (quoted by BUSHMAKIN) weighed twenty six brains and found only slightly smaller averages. Taking the average of both authors, the average male weight is 1485, the female 1438 gr. In all females weighed by BUSHMAKIN the brain was heavier than the average russian female brain weight although russian women (and men) are taller.

BUSHMAKIN considers the generally high brainweight and greater cephalization coefficient in Buriates as a tribal character (cf. p. 204, where the cephalization coefficient of the Eskimo, is discussed). He is inclined to correlate the very small sexual differences with the fact that Buriate women for ages have done the same work as men.

In the gyration of the brain the author found the transverse fissures prevailing (as often found in brachycephalics, CALORI, RETZIUS). Related to this may be the fact that the parieto-occipital often extends far on the convexity, not rarely connected with the transverse and anterior occipital, which again may join the superior temporal. He erroneously considers this combination as equivalent to the simian fossa thus including in it the anterior occipital fissure and not referring to ELL. SMITH's lunate sulcus. The insula is nearly always tigthly closed. This was also the case in my Tatar. The central sulcus — which in Swedes (RETZIUS) indents the medial margin in 80%, in Buriates was found to indent in 59%. (In the Dutch, this figure is the same as in the Swedes). The author found the *midfrontal sulcus* well pronounced which is the more striking as transverse fissures prevail in Buriates. The intraparietal was often divided in segments and the olfactory tracts seem to be more than usually well developed.

The brain of the *Lapps* has been described only once, by RETZIUS [2]), who apparently had a well preserved specimen at his disposal. Calculating the sagittal indices on his figures I found that this brain shows the same sagittal indices that I found to prevail in the Northern Chinese, a high rounding, steep frontal and occipital angles, a fairly high callosum index, small stem angle, and narrow

[1]) BUSHMAKIN. Characteristics of the Mongol race. American Journ. of physic. Anthrop., vol. 12, 1928.

[2]) RETZIUS. Das Gehirn eines Lapländers. Festschrift für Virchow, 1891.

fossa interpeduncularis, but it is brachencephalic not mesencephalic as most of the latter are.

The *Chinese* brain is first described by PARKER and MILLS [1]), BENEDIKT [2]) and DERCUM [3]).

The brains were those of coolics and consequently were probably Southern Chinese brains (the Northern Chinese migrated very little at that time).

In these communications the authors point to what is called by DERCUM the eversion i. e. the sloping character of the orbital surface of the frontal lobe. Both BENEDIKT and DERCUM also observed an exquisite inward turned position of the temporal lobe. The latter was further struck by the great sinuosity of the fissures, and by the fact that the frontal lobe is strongly convoluted, and characterized by short longitudinal fissures frequently broken by transverse ones. The same was observed by BOND [4]).

The Chinese brain described by LEFFINGWELL HATCH [5]), judging from his figures, had not been fixed very well. He pointed out that the "plis de passage supérieur interne" lies at the surface on both sides.

SCHUSTER's work [6]) contains a detailed description of the fissures, but does not tell much about the general morphology. In his brief description of seven Chinese brains from Singapore, HARPER [7]) first called attention to the *lunate sulcus*, also found by myself and especially described by SHELLSHEAR.

In 1911 and 1920 COLE [8]) gave descriptions of asiatic brains, among which some Chinese. For his description I refer to the original.

---

[1]) PARKER and CH. K. MILLS. Preliminary study of a Chinese brain. Journ. of nerv. and ment. disease, Vol. XIII, 1886.

[2]) BENEDIKT. Drei Chinesengehirne. Wiener mediz. Jahrb. 1887.

[3]) DERCUM. A description of two Chinese brains, Journ. of nerv. and ment. diseases, Vol. XVI, 1889. DERCUM. Note on a Chinese brain. Ibidem, Vol. 19, 1892.

[4]) BOND. Observations on a Chinese brain. Brain, Vol. VIII, 1891.

[5]) J. LEFFINGWELL HATCH. Studies upon the Chinese brain. Intern. Monatschr. f. Anat. und Physiol. Bnd. VIII, 1891.

[6]) SCHUSTER. Description of 3 Chinese brains presented by Dr. F. W. MOTT to the Museum of the Royal College of Surgeons, Journ. of Anat. and Phys. Vol. 42 & 43. Of these brains A. MARIE gave some linear measurements and CUNNINGHAM's Sylvian angle without, however, reaching a definite result. (see Archives de Neurologie, 1914).

[7]) HARPER. Notes on the weight and convolutional pattern in 7 Chinese brains. Arch. of Neur. and Psych. London, Vol. III, 1907.

[8]) COLE. Remarks on some points in the fissuration of the cerebrum. Journ. of Anat. and phys. Vol. 46, 1911--1912 and: Fissural pattern in four

SHELLSHEAR [1]), who examined many brains found the lunate sulcus more anthropoid in type in the Chinese than in the Egyptians, described by ELL. SMITH, the s. occipitalis transversus being more often confluent with it.

A valuable description of the entire convolutionary pattern was given by KURZ [2]), who first studied a female brain of 35 years, a male of 25 years and a neonatus, and later described three adult and seven children's brains, all from Shangai.

As characteristics he mentions the sloping condition (concavity) of the orbital surface, (cf. DERCUM) a distinct rostrum orbitale, a pronounced curvature of the frontal lobe, a strong inward curvature of the temporal poles, (cf. BENEDIKT and DERCUM) and a strong mesial concavity of the temporo-occipital lobe; further, a steep occipital lobe with a steep gyrus hippocampi, (uncus?) a partly exposed insula Reilli (in 60% of his brains!), a narrow fossa interpeduncularis, and a not very obtuse angle between the oblongata and the basis cerebri. In the general fissural pattern he was struck by a number of transverse anastomoses on the frontal lobe (cf. PARKER, MILLS and DERCUM), a long s. frontalis medius, a s. frontalis inferior, either merging into the sulc. fronto-orbitalis (subfrontalis mihi?) or developing in that direction, a very frequent division of the strongly arched intraparietal in its three constituents [3]) (see above BUSHMAKIN), a simian sulcus which, however, he describes in a similar way as BUSHMAKIN does in Buriates, not referring to SMITH's lunatus [4]).

The gyrus frontalis superior and pars superior gyri frontalis medii,

asiatic brains (among which one Chinese and one Japanese). Engl. Journ. of Anat. Vol. 54, 1920.

[1]) SHELLSHEAR. The occipital lobe in the brain of the Chinese with special reference to the lunate sulcus. English Journ. of Anat. Vol. 61, 1926.

[2]) KURZ. Zwei Chinesengehirne. Zeitschr. f. Morph. und Anthrop. Bnd. 16, 1913; Das Chinesegehirn. Zeitschr. f. Anat. und Entw. Gesch. Bnd 72, 1924; Das Gehirn der Gelben und die mehrstämmige Abkunft der Menschenarten. Anat. Anz. Bnd. 58.

[3]) For statistical figures concerning the chief sulci of the parietal and temporal lobes in the Dutch, see: WANG HWEI-WEN and KAPPERS. Some features of the parietal and temporal lobes of the human brain and their morphological significance. China medical Journal, Sept. 1924. See also SHELLSHEAR: The Caduceus 1926: The inferior parietal lobe of the brain.

[4]) I do not agree with his interpretation on this point, nor with BUSHMAKIN's. In KURZ' fig. 24 and 53 a distinct lunate sulcus is seen surrounding an ypsiliform and postcalcarine fissure.

had only a few accessory convolutions, the operculum triangulare is not so well separated from the pars orbitalis and there was a certain lack of accessory convolutions in the upper part of the temporal lobe.

He found the centralis indenting the mesial margin only in 15%. KURZ believes that many of these peculiarities point to a lower organization of the Chinese brain, resembling somewhat the brain of the eastern anthropoid, the Orang utan, which also possesses a strongly arched frontal lobe, a concave orbital plane, a distinct orbital rostrum and an inward bent temporal lobe. Adding to these encephalic features some somatic ones concerning the hair, the profile of the face and the serological reaction of the blood [1]), KURZ is inclined to the view that the Chinese spring from an Orangoid ancestor, accepting with MELCHERS and KLAATSCH the theory of polyphyletic descent of man, as CROOKSHANK [2]) does in England.

I also found that several of the characteristics mentioned above in reality often occur in the Chinese brain e. g. a concavity in the orbital plane with an orbital rostrum, though less than in prehistoric brains, the round shape of the frontal lobe; the inward curvature of the lower part of the blunt temporal pole; further, the depressed occipital lobe, with a strongly pronounced medial concavity for the cerebellum, and a narrow fossa interpeduncularis. Mrs. VAN BORK [3]) found a bulging parietal lobe, hooklike calcarine, a steep callosomarginal fissure, a steep uncus, often indented by a small groove, probably caused by the anterior petrosal edge of the tentorium. She did not however (nor did I) find a more frequently exposed insula or failing indentation of the central sulcus. Comparing the Orang utan brain (fig. 113) with that of the

---

[1]) The general facts are these, that of the two factors A and B, acting the largest part in the anthropological serum reaction, the North-west Europeans have more A, the Mongols more B. Now in 40 Chimpanzees examined the factor B is never found, while in five Orangs examined by LANDSTEINER, two belonged to the group A, three to the group B, (quoted from HIRSZFELD, Les groupes sanguins dans la biologie et la médicine. Institut intern. d'Anthropologie, Session d'Amsterdam, 1928).

[2]) CROOKSHANK. The Mongol in our midst. London 1925.

[3]) Mrs. A. J. VAN BORK—FELTKAMP. Inaugural Dissertation, Amsterdam, 1930. This study of about sixty Chinese brains is the best given till now.

Fifty of these brains were presented to my institute by Dr. SHELSHEAR, to whom I express also here my thanks.

Chinese (fig. 135), their resemblance seems rather farfetched, and not more pronounced than with the Chimpanzee. However attractive the polyphyletic theory of the descent of man may be, and without excluding its possibility, the fact that the Chinese brain in its *general morphology* bears much more resemblance to certain developmental stages of the human brain in general than to any anthropoids brain, leads me to examine, another possibility to explain some of the peculiarities of the Chinese encephalon.

Without entering again into details of fissuration, I shall discuss some of the general morphological features of the Chinese brain, which seem to support another factor in the evolution of races, though it does not ipso facto exclude a polyphyletic origin of races.

Brain-indices.	Chinese.	Dutch brachy-cephalics.	Fetuses and neonati.	Dutch dolicho-cephalics.
General height index ...	0,535	0,522½	0,586	0,491
Occipital index.........	1,56	1,45	1,47	1,19
Temporal depth index ..	0,166	0,160	0,157	0,145
Temporal length index..	0,780	0,760	0,7—0,758[1]	0,748
Frontal length index ...	0,343	0,363	0,326	0,346
Frontal height index ...	0,470	0,478	0,503	0,443
Callosum height index ..	0,383	0,382	0,402	0,321
Sternangle	101,6°	100,3°	96°	106°

Calculating the sagittal brain indices and angles, described above (see p. 217), for the Chinese, and comparing them with brachencephalic and dolichencephalic Dutch, and with Dutch newborns, it appeared to me that all sagittal indices found in fetuses and neonati, are larger than those in the dolichocephalic Dutch. They come nearer to those of our brachycephalics and especially to those of the Chinese.

The greater similarity of sagittal indices of neonati to those of brachycephalics than to dolichocephalics corresponds with researches on the skull. RETZIUS found that Swedish fetal skulls approach more brachycephaly than adult ones do (cf. MARTIN [2]). Similarly

---

[1]) 0,7 is the average index in the last two months before birth, 0,758 in the first two motnhs after birth.

[2]) MARTIN. Lehrbuch der Anthropologie. Fischer, Jena, 1914, p. 605.
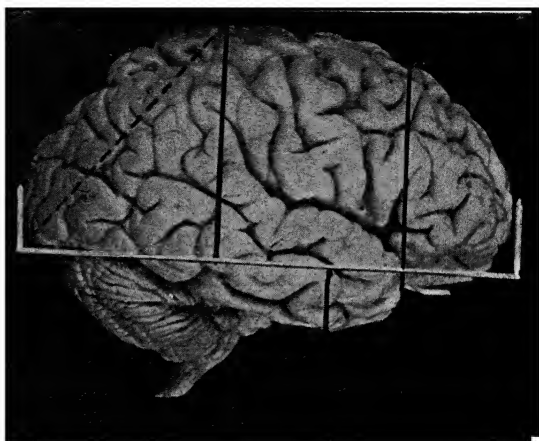
Fig. 133. Dolichocephalic Dutch brain; right
hemisphere.
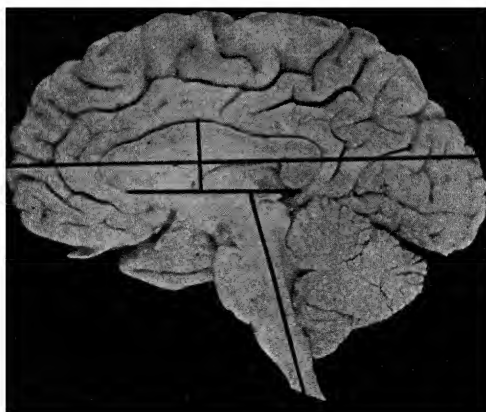
Fig. 134. Same hemisphere as above, medial aspect.
Note the large stemangle, horizontally arched
calloso-marginal and horizontal calcarine fissure.
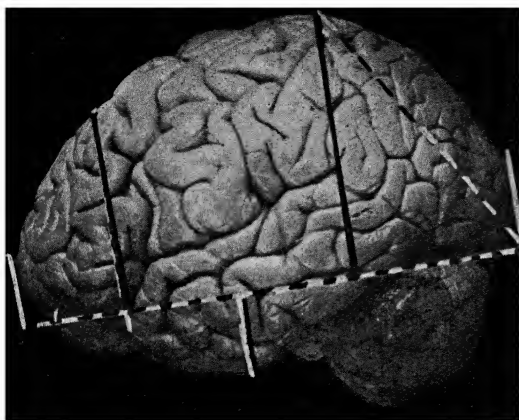
Fig. 135. North Chinese brain, left hemisphere.
Note the rostrum orbitale, steep occipital and
round frontal pole.
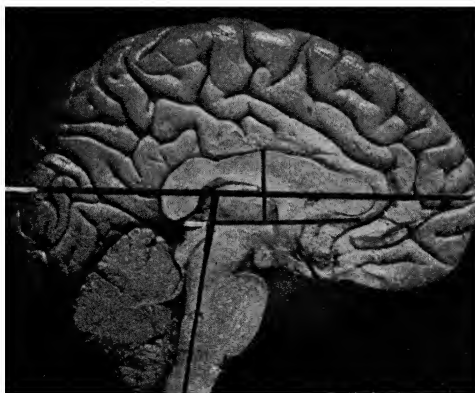
Fig. 136. Same hemisphere as above, medial
aspect. Note the small stemangle, narrow fossa
interpeduncularis, steep calloso-marginal and
hooklike calcarine fissure.
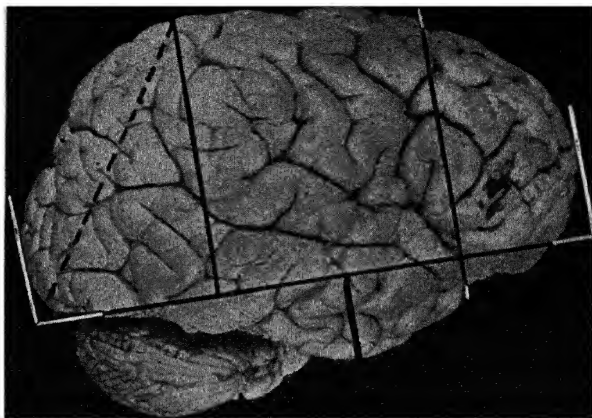
Fig. 137. Brachycephalic Dutch brain, right hemisphere lateral. The rostrum orbitale is fairly large, the occipital pole steep, the frontal round.
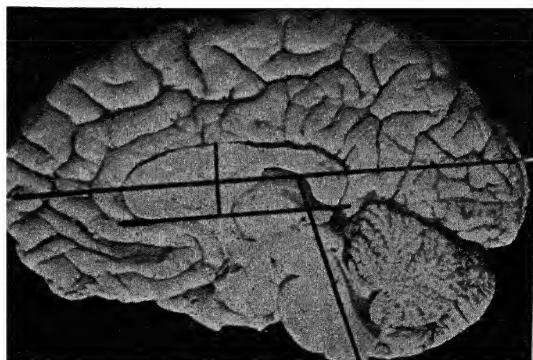
Fig. 138. Same hemisphere as above, medial aspect.

Fig. 139. Child one month old. Note the large rostrum orbitale, the steep frontal and occipital pole.
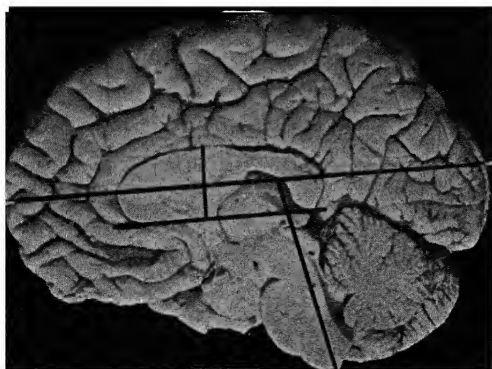
Fig. 140. Same hemisphere as above, medial aspect. Note the small stemangle, narrow fossa interpeduncularis and hooklike calcarine.

Röse [1]), in Swiss schoolboys at Schaffhausen, stated a decrease from 84 to 82,5 between 8 and 18 years, and Frets [2]) in Dutch boys found a decrease from 82,14 to 79,27 from the first to the 20th. year.

Besides Dutch fetuses and brachycephalics are also more hypsicephalic than fullgrown Dutch. Correlated with this is the fact that their sagittal indices approach those of the Chinese (see p. 279).

Striking in this respect is the Chinese callosum index which, though not attaining the same height as in the new born Dutch is not less that 0.62 higher than in Dutch dolichocephalics and (exceeding the index in the Orang) is about equal to Dutch brachycephalics.

Also Ma Wen Chao [4]) found the average callosum index largest in the Chinese (fig. 141), somewhat less in the Philippino's, and least in dolichencephalic Dutch (fig. 142). Besides this he found correlated differences with the (septum and) fornix, which on an average shows a more acute angle with the genu callosi at the level of the anterior commissure in the Chinese than in Dutch dolichencephalics.

On page 220 I mentioned that both my *Rolandic and Sylvian angles* are smaller in newborn Dutch brains than in the adult, thus confirming Cunninghams statements. As especially my Rolandic angle increases, the inclination angle between both fissures decreases with the adult. Similarly in the Chinese (and brachycephalics) the Rolandic and Sylvian angle are usually smaller than in Dutch dolichencephalics (cf. fig. 133 with fig. 135 and 137). The *inclination angle* remains somewhat larger chiefly on account of the steeper Rolandic fissure, so that also in this respect a more fetal character occurs in the Chinese which may be equally correlated with their hypsicephaly.

In view of these facts we should consider the possibility to use Bolk's theory of *fetalization,* or *juvenilization,* as I should prefer to call it, to explain the general morphology of the Chinese brain,

---

[1]) Röse. Beiträge zur europäischen Rassenkunde. Arch. für Rassenbiologie Bnd. 2 (p. 689), 1905; Bnd. 3 (p. 42), 1906.

[2]) Frets. Heredity and Headform in man. Genetica, Vol. 3, p. 193.

[3]) Reuter noted a greater hypsicephaly in Pommerian children compared to adults (Martin, Lehrbuch der Anthr. page 606) and Frets found the same in Dutch newborns.

[4]) Ma Wen Chao. A comparison of the form of the callosum and septum in the Chinese, Philippino- and Dutch Brains. Proceed of the Kon. Akad. v. Wetensch. Amsterdam, Vol. 30. 1927.
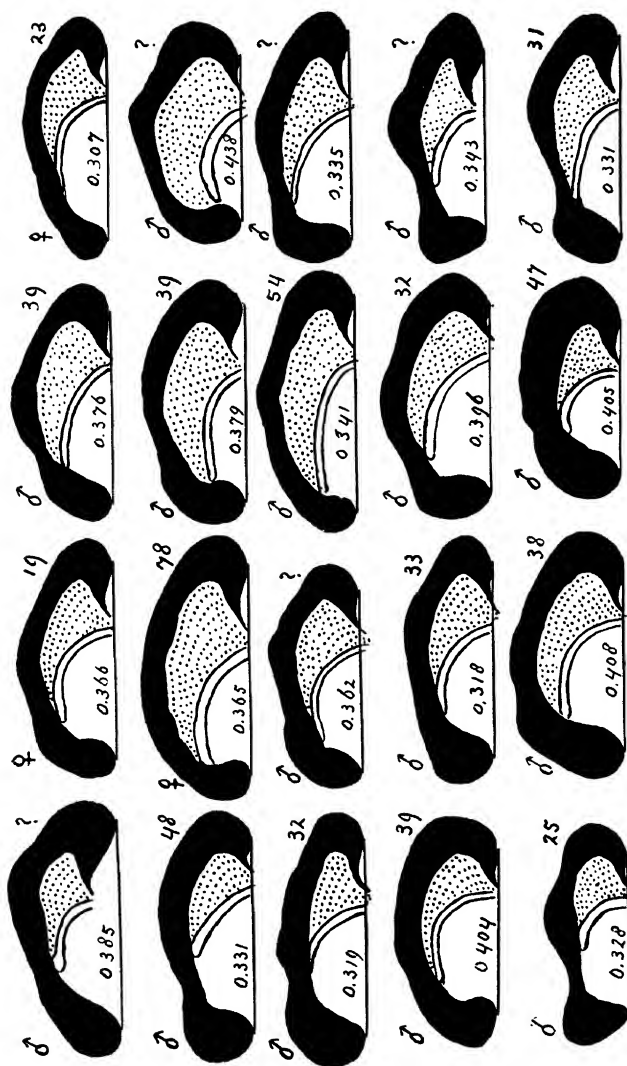
Fig. 141. Twenty Chinese corpora callosa after MA WEN-CHAO. On the left of the callosa the sex, on the right the age of the individual is mentioned. The figures inside give the callosum height index (average index 0,361).
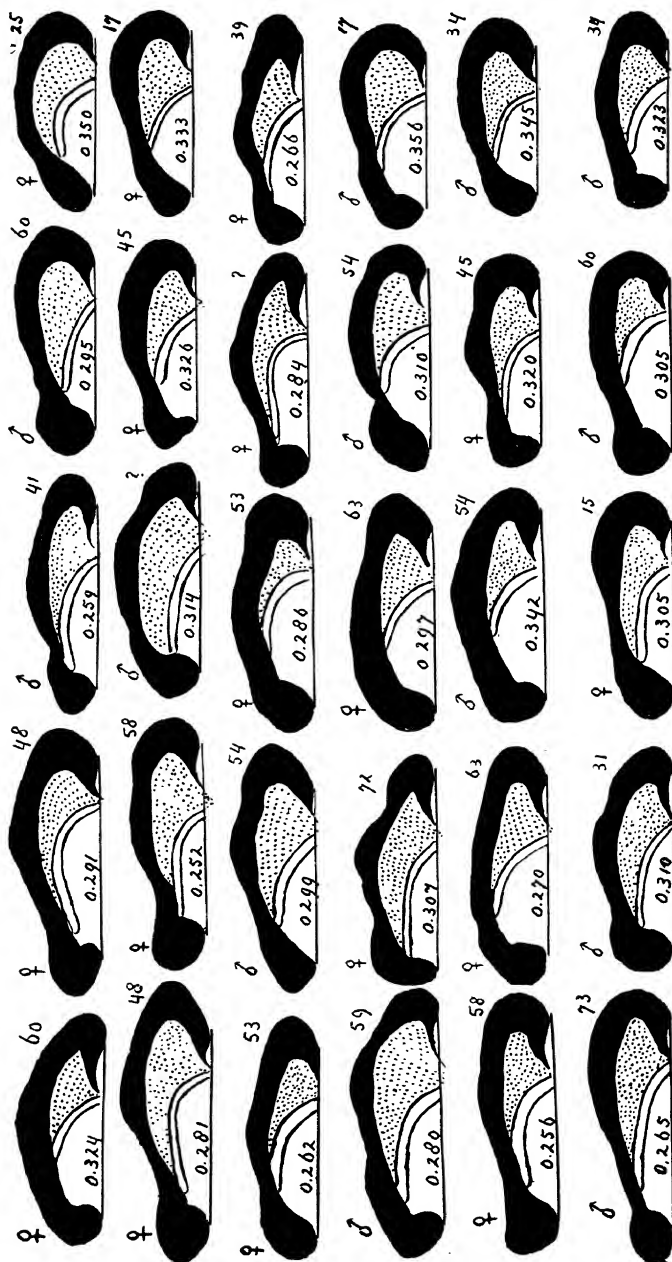
Fig. 142. Thirty corpora callosa of dolichencephalic Dutch after MA WEN CHAO. On the left of the callosum the sex, on the right the age is indicated. The figures inside give the callosum height index (average index 0,300).

the more so as not only the height indices of the brain and callosum, blunt temporal lobes, larger rostrum orbitale (cf. figs. 133, 135 and 139) and smaller stemangle remind us of fetal or neonatal conditions, but also the relation of the spinal and bulbar parts of the hypoglossus nucleus in the Chinese is similar to that in Dutch newborns (VERMEULEN [1]).

Besides, also other parts of the Chinese body show characteristics, that may be explained as persistent younger features.

Thus BIRKNER [2]) found the size of the platysma to be unusually large, extending as a rather closed plate over the face, a feature which, among Europeans, occurs only in children.

The zygomaticus and the quadratus labii superioris persist as rather closed muscle plates, enlarged by irradiating bundles from the orbicularis oculi to the mouth angles. This also occurs in young European children. Similarly TOKUYASO KUDO [3]) who compared the facial musculature in 15 Japanese, 3 Chinese and 5 Europeans, stated (l. c. p. 669) that "the Japanese and Chinese differ from the Europeans by a somewhat lesser differentiation, a tendency of single muscles to fuse superficially into a single plate. This tendency is stronger in the Chinese than in the Japanese". He adds to this: "in Mongolians as a race the three parts of the quadratus labii superior fuse into a single plate and the zygomaticus, constantly present in Mongolians, is distinguishable with difficulty from the neighbouring muscles" (l. c. p. 671). BOLK [4]), though generally inclined to regard the Nordic race as the most fetalised type, has pointed out himself, however, that the Mongoloid fold and epicanthus, frequent characteristics of the Chinese upper eyelid, are encountered as a fetal phenomenon in Europeans; similarly the deep nose root and protusio bulbi.

SHELLSHEAR [5]) (l. c. p. 7) has remarked that the parenchyma of the thymus gland persists up to a later age than in Europeans. The ages corresponding to the European type are not in agreement with the findings in the Chinese. In them the young condition, instead of changing at 20, runs on till about 25 years of age (cf. herewith, however, HAMMAR's excellent monograph) [6]).

[1]) Personal communication. (Cf. also VERMEULEN. Proceed. of the Kon. Akad. van Wetensch. Amsterdam. Vol. 27, 1924.

[2]) BIRKNER. Die Anthropologie der Mongolen. Arch. für Rassen und Gesellschaftbiologie, Jahrg. 1, 1904, p. 817.

[3]) TOKUYASO KUDO. The facial musculature of the Japanese. Journ. of Morphology. Vol. 32, 1919, p. 637.

[4]) BOLK. Over Mongolenplooi and Mongoloide idiotie. Ned. Tijdschrift v. Geneesk. 1ste helft 1923, Afd. 3. See also: Over de oorzaak en de beteekenis van het niet-sluiten der schedelnaden bij den Mensch. Ibidem 1926, 2e helft.

[5]) SHELLSHEAR. The thymus gland in the Chinese. China med. journal, Aug. 1924.

[6]) HAMMAR. Die Menschenthymus in Gesundheit und Krankheit. Zwei Teile, Akad. Verlag, Leipzig 1926—1929. HAMMAR showed that great variations may also occur in Europeans.

Another somatic peculiarity of the Mongols [1]) corroborating our view, is the fact that the proportion between the length of the legs and that of the trunk favors the trunk with the Mongols more than with the Caucasians.

SHIROKOGOROFF and APPLETON [2]) point out (l. c. p. 110), that — especially among the Northern Chinese — the hair growth is strongly retarded compared with Europeans. In men this holds good as well for the beard as for the pubic hair, and in women it applies to the pubic and axillary hair. They say; "It is very characteristic in Chinese women that thay have sometimes no axillary and pubic hair at all (l. c. p. 110)".

Dentition among the Chinese also seems to follow a different periodicity from that of Europeans: "there is a retardation of full dentition (except in the third molar) which continues after the age of 15 years. On the other hand there is a premature (comparatively with Europeans) appearance of the second and third molars".

Finally, my attention was called to a fact that ossification in the Chinese occurs at a somewhat later period than in Europeans.

If we are allowed to include the Japanese in this consideration I may also mention the observation made by TAGUCHI [3]) that a larger quantity of brain-weight is obtained after childhood in the Japanese than in the European (German), while the Japanese also reach their adult somatic weight and length at a later period than Europeans (BAELZ [4])).

All these factors seem to agree with SHELLSHEAR's statement (l. c. supra p. 10): "their anthropological type might almost be regarded from an European standpoint as a childlike type", an opinion expressed already in 1860 by CHAMBERS [5]), on the basis of the facial characteristics of the Chinese.

They also support my view that the general form of the Chinese brain may be explained from this standpoint.

In this respect also the *stem angle*, and the *narrow fossa interpeduncularis*, resulting from it, are important.

---

[1]) STRATZ. Wachstum und Proportionen des Menschen vor und nach der Geburt. Arch. für Anthropologie. N. F. Bnd. 8, 1909, and: Grösse und Proportionen der Menschlichen Rassen. Ibidem Bnd. 10, 1911. See also OBERMAIER Der Mensch aller Zeiten, Bnd. 2, and STEVENSON China med. Journ., 1925.

[2]) SHIROKOGOROFF. Process of physical growth among the Chinese. Vol. 1. The Chinese of Chekiang and Kiangsu measured by Dr. APPLETON. The Commercial Press, lim., Shanghai, China, 1925.

[3]) Quoted from SPITZKA. The brain weight of the Japanese. Science, Philadelphia, 1903.

[4]) Die körperlichen Eigenschaften der Japaner. Mitt. der Deutschen Gesellsch. f. Natur und Völkerkunde. Ost Asians, Erster Teil, Bnd. III (1880—'84), 2ter Teil, Bnd. IV (1884—'88).

[5]) CHAMBERS. Vestiges of the natural history of creation. London, 1860, p. 232: "The Mongolian is an arrested infant newly born".

The stem angle in the Chinese (similarly in RETZIUS Laplander [1]), also a Mongol, is smaller than in dolichocephalic Dutch. It is also small in Dutch brachycephalics (Alpines) but smaller still in the fetus. This again apparently is correlated with the form of the skull, in casu the location and the inclination of the foramen magnum.

BOLK [2]) has drawn attention to the fact that the foramen magnum occupies a relatively more frontal position at the end of fetal life than in the adult. As my stem axis runs through the foramen magnum, it is not surprising, that in the fetus it runs steeper than in the adult, where it has a more backward inclination.

It is interesting, that BOLK also found the inclination of the foramen magnum to be turned more frontally in brachycephalic than in dolichocephalic Dutch, as I did for the stem axis of the brain.

Considering all the other relations in the general outlines of the Chinese brain, BOLK's principle of fetalisation [3]) or retardation, as he also calls it, should be very seriously considered in explaining its morphology, the more so since BOLK's principle, together with other factors, seems to lie at the bottom of the differentiation of the genus homo as a whole from a common stem with anthropoids.

It was for this, its *anthropogenetic value*, that BOLK created his theory The intrahumane differentiation is only a secondary consequence.

It is well worth while to resume briefly BOLK's arguments for assuming fetalization as a prominent factor in *anthropogenesis*.

The facts he started from are these: 1⁰. the anthropoid and the human newborns are anatomically much more similar to each other than the adults; 2⁰. the differences arising in later age are such that the morphological features of the anthropoid deviate more and more from the fetal features, developing in a very specialized or "propulsive" way, as he calls it, while those of adult man retain a greater resemblance to juvenile characteristics. So the adult human sacrum still has the curved form as in fetal anthropoids and fetal man. Similarly, while the newborns of both are unpigmented and covered only with little hair, the anthropoid developes much pigment and hair, while men develop less. Also the human ear keeps its fetal form more than in the adult anthropoid, etc.

---

[1]) Cf. RETZIUS. Das Gehirn eines Lappländers. Festschrift für Virchow 1891.

[2]) BOLK. On the position and displacement of the foramen magnum in Primates, Proceedings of the Kon. Akad. v. wetensch. Amsterdam, Vol. 12, p. 362, (1909); On the slope of the foramen magnum in Primates. Ibidem, p. 525, (1909).

[3]) The most complete account of his theory is given by BOLK in: Das Problem der Menschwerdung. Gustav Fischer. Jena, 1926 and further in the Proceed. of the Koninkl. Akademie v. Wetensch. Amsterdam 1926—1927.

An important point is the relation of the facial part of the skull to the endo-cranial part. This is more orthognath in both at birth, and keeps that character very much in men while in anthropoids a strong prognathism developes. In connection herewith the relatively large endocranial capacity in both newborns may also be mentioned [1]), this capacity remaining much greater in man than in anthropoids. Though all the arguments advanced by BOLK may not stand criticism (see NEUVILLE [2])), there are certainly a great many points in which adult men keep a greater resemblance to fetal conditions than anthropoids do, thus developing in what BOLK called a conservative way, while the anthropoids develop along more specialized or propulsive lines.

As KEITH [3]), BOLK [4]) is inclined to attribute a great influence to endocrine secretions in explaining racial differentiations, as these secretions have a great influence on pigmentation, hair growth, skeletal relations and also on the functional abilities, and, conse-quently, on the growth of the brain. The endocrine, or metabolic theory in general, also may explain the occurence of analogous features in different races, without accepting genetic relationships. So it may explain that brachycephaly, or some degree of prognathism or pigmentation may occur in different groups of men as a symptom of convergency, arising in each race separately, in consequence of analogous changes in endocrine secretion, the influence of which is so clearly demonstrated among animals in laboratory experiments (STOCKARD [5])).

It is, however, evident that before accepting endocrine factors in racial questions they have to be proved physiologically and that we should inquire by what influences eventual endocrine differences may be induced. Here we have to look also at that new field of anthropological physiology, that studies the influence of the medium via the mother on the fetus.

The influence of the medium via the mother seems to receive

---

[1]) Cf. also ANTHONY et COUPIN. Introduction à l'étude du dévelopement pondéral de l'encéphale. l'Indice de valeur cérébrale au cours de l'évolution individuelle. Zagreb 1925 -1926.

[2]) NEUVILLE. De certaines charactères de la forme humaine et de leur cause. l'Anthropologie, Tome 37, 1927.

[3]) KEITH. The differentiation of mankind into racial types. Presidential address of the British association for the advancement of sciences. Section II, 1919. See also KEITH. Concerning man's origin, Forum series, 1927.

[4]) BOLK. The part played by the endocrine glands etc., The Lancet, 1921.

[5]) STOCKARD. Human types etc. American Journal of Anatomy, Vol. 31, 1923.

support in the work [1]) of Boas, who found that marked morphological changes in the children may occur by endocrine and emotional conditions of the mother.

This could be observed in such children whose immigrant mother passed her pregnancy in the new country, in contrast to those born before.

So he found that the average index of the male Sicilians, 77,7 in Europe, is 81,5 with those born in America. With the Jews this index decreases from 83 to 81,4 under the same conditions.

In both cases he thus found an approach to a similar figure.

N. HIRSCH [2]) in his researches on the cephalic index of American-born children of three foreign groups confirms Boas' findings, and pleads for the influence of endocrine secretion correlated with psychological conditions on the mother and children.

Also some of the results obtained by APPLETON in his study on the growth of Chinese children in Hawaii seem, in a general way, to confirm Boas' statements as they show the influence of environment on somatic development [3]).

Returning to the fetal character of the general morphology of the Chinese brain, I still want to remark that some general morphological characteristics as found in the Mongol brain also occur in Mongoloid idiocy cf. H VOGT [4]), VAN DER SCHEER [5]), CROOKSHANK [6]), BROUSSEAU and BRAINERD [7]).

Through the courtesy of Dr. VAN DER SCHEER I could convince myself that here also we may find a well pronounced orbital rostrum,

---

[1]) Boas. Changes in bodily form of descendants of immigrants. Report of the immigration commission Washington, 1911 and American anthropologist, Vol. 14, 1912.

[2]) Am. Journ. of Phys. Anthrop. Vol. X, 1927.

[3]) APPLETON. Growth of Chinese children in Hawaii and in China. Am. Journ. of physical Anthrop. Vol. X, 1927 and Growth of Kwantung Chinese in Hawaii Ibidem, Vol. XI, 1928.

[4]) H. VOGT. Die angeborenen Defekte und Entwicklungsstöhrungen des Gehirns, in the ,,Handbuch der Neurologie", of LEWANDOWSKY, Bnd. III.

[5]) VAN DER SCHEER. Beiträge zur Kenntnis der Mongoloiden Missbildung (Mongolismus). Abhandl. aus der Neurologie, Psychiatrie and Psychologie und ihren Grenzgebieten, Heft 41, 1927.

[6]) CROOKSHANK. The mongol in our midst. London, 1925.

[7]) BROUSSEAU and BRAINERD. Mongolism. A study of the physical and mental characteristics of mongolian imbeciles, London Baillière, Tindel and Cox, London 1928.

a strikingly inward turned temporal pole, smaller stem axis and narrow peduncular fossa (V. D. SCHEER).

As these idiots may be born from dolichocephalic as well as from brachycephalic parents, we have here a demonstration that retardation of development may give rise to mongoloid characteristics.

For the rest it goes without saying that the so-called mongoloid idiot is a pathological product, in which other factors than the mongoloid morphology are responsible for the idiocy, the pathological changes in the brain and in the body being numerous (cf. H. VOGT, VAN DER SCHEER).

On the other hand the Chinese cultural history is not only normal but in many respects very precociously developed.

I must [1]) also contradict CLAPHAM's [2]) supposition concerning the inferior development of the cortex in Chinese brains.

I have defined in a direct way the quantity of cortex per hemisphere [3]) of three adult Dutch and Chinese brains of about equal total weight.

Race Sex Age.	Total brain weight	Weight left Hem.	Weight right Hem.	Cort. left Hem.	Cort. right Hem.	Average percent p. Hem.	Total Cort. on tot. brainw.
Eur. 1 ♂ 29 j.	1068	474,5	477,5	237	238,5	49,96%	44,5%
Eur. 2 ♂ 42 j.	1375	618	613	299	297	48,39%	42,8%
Eur. 3 ♂ 18 j.	1360½	621	622	331	336	53,60%	48,9%

Average percentage cortex Dutch, per Hem 50,65%

per tot. Br. 45,0%

Race Sex Age.	Total brain weight	Weight left Hem.	Weight right Hem.	Cort. left Hem.	Cort. right Hem.	Average percent p. Hem.	Total Cort. on tot. brainw.
N. Chin. ♂ ?	1014½	430	437,5	218	212,5	49,31%	42,43%
N. Chin. ♂ ?	1344	576	584	300	297	51,48%	44,42%
N. Chin. ♂ ?	1425½	615,5	638	313,5	320	50,51%	44,15%

Average percentage cortex Chinese, per Hem 50,45%

per tot. Br. 43,8%

[1]) ARIËNS KAPPERS. The relative weight of the brain cortex in human races and in some animals and the asymmetry of the hemispheres. Proceed. of the Kon. Akad. v. Wetensch., Amsterdam, Vol. 28, 1925.

[2]) CROCHLEY CLAPHAM. On the brain weight of some Chinese and Pelew islanders. Journ. of the Anthrop. Soc. of Great Britain and Ireland. Vol. 7, 1878.

[3]) The body weights in these individuals were about the same. Evidently the relation between cortex and bodyweight is the chief point, not the relation between cortex weight and brainweight which is even larger in idiots (TAFT) and small animals.

As appears from the adjoining table in the Dutch the average percentage of cortex is 45,0 % per total brainweight; in the Chinese an average percentage of 43,8%. This is practically the same, as in both races the differences fall within the limit of individual variations.

As the relation between brainweight and bodyweight does not differ much in the Chinese and Dutch used for this purpose, it follows that also the relation between cortex weight and bodyweight is about the same.

Finally, I must contradict TOPINARD's and HARPER's assertion, that the cerebellar weight on the total brainweight is less in the Chinese than in the European. For this purpose I compared 22 Chinese with 25 Dutch brains, and obtained the following figures[1] — to which I add, for the sake of completeness, those concerning eight Japanese brains, kindly sent to me by Prof. G. FUSE (Sendai).

Specimens.	Total brain weight.	Cerebell. weight.	Cerebell. percent.
25 Dutch	1266,1 gr.	131,7 gr.	10,399
22 Chinese	1217,1 gr.	126,5 gr.	10,39
8 Japanese	1212,31 gr.	125,9 gr.	10,38

This difference is too small to be of any importance, the less so, since I found with both races a variation margin of 4,2% [2]).

I should like to remark that these researches on the general morphology of the Mongol brain and that of the Dutch brachycephalics do not contradict the generally accepted relation between the population of middle and northern Asia and the European alpine race, to which our brachycephalics may belong.

Our dolichocephalics are largely Nordics, a race whose ancestry still is uncertain. BOULE supposes that they are not related to the Cro-Magnon proper but existed in central Europe contempory with the reindeerman, and that in

[1]) ARIËNS KAPPERS. The relation of the cerebellar weight to the total brain weight in human races and in some mammals. Proceed. of the Kon. Akad. v. Wetensch. Vol. 29, 1926. The weighing of the Dutch and the Chinese brains was done in the same standard fashion, i. e. without pia and with emptied ventricles. The provisional determination with the Japanese was made with pia and undivided hemispheres. This perhaps may explain their slightly lower percentage than with the Chinese, as the forebrain ventricles may contain 34 cM³. fluid (HARVEY).

[2]) A similar margin in the cerebellar percentage was found by Dr. I. KELLERS PUTNAM in mammals. The proportion of cerebellar to total brainweight in mammals. Proc. Kon. Akad. van Wetensch. Amsterdam, Vol. 31, 1928.

neolithic times they were especially abundant in central Russia. Their history and spread seems to coincide with those of the Aryan languages.

The more pigmented and smaller Southern European and circummediterrean dolichocephalics, the Homo mediterraneus is hardly represented in Holland. According to BOULE they are closely related to North African relics of the reindeerman (l. c. p. 350 — c. f. also TAYLOR).

The *Japanese* according to KOGANEI form a link between the real Mongol and Malay races, in which the latter — a special mongoloid branch according to some authors — dominates.

The brain weight of the Japanese, according TAGUCHI [1]) is 1367 gr. for males, 1214 for females thus showing a great sex difference.

In their general morphology as expressed by my indices they seem to approach the Chinese group, with whom they also share he average skull index (78.3 for men, 79.7 for women; ADACHI).

The gyration of the Japanese forebrain has been described by SERGI [2]), HARA [3]), HAYASHI and NAKAMURA [4]). The latter found the lunate sulcus to occur in 40—60% of the Japanese (cf. also KUHLENBECK [5])). SHIMADA [6]) has given recently data on the morphology of the cerebellum, fossa rhomboidea and pons, FUSE [7]) and

If, with a larger material, it might appear that the slightly lower percentage of the cerebellar weight in the Mongols is constant, this might perhaps also plead in favour of fetalization, as we know from PFISTER'S [1]) researches that the cerebellar percentage is lower with fetuses, and only rises to 10,4 per cent 6 or 7 months after birth. Arch. für Kinderheilkunde, Band 23.

[1]) TAGUCHI. On the weight of the encephalon in the Japanese. Neurologia, Vol. I, 1903. Quoted from SPITZKA. Brain weight in the Japanese, Science Philadelphia, 1903.

[2]) SERGI. Note morfologiche sulla superficie metopica del lobo frontale in cervelli di Indiani e di Giapponesi. Ric. fatte nel laborat. di anat. norm. di Roma etc. Vol. 17, 1913.

[3]) HARA. Ueber die Hirnoberfläche der Japaner (japanisch) Mittl, der med. Gesellsch. zu Tokyo, Bnd. 27, 1913.

[4]) HAYASHI and NAKAMURA. Ueber die Hinterhauptlappen des Japaner-gehirnes. Mittl. aus der med. Fak. der Kaiserl. Univ. zu Tokyo, Bnd. II, 1914.

[5]) KUHLENBECK. Bemerkungen zur Morphologie des Occipitallappens des menschlichen Grosshirns. Anat. Anzeiger Bnd. 65, 1928.

[6]) SHIMADA. Beiträge zur Anatomie des Zentralnervensystems der Japaner. Four contributions. Acta schol. med. Kyoto 1916—1922.

[7]) FUSE and YAMAMOTO Beiträge zur makroskopischen Anatomie des Truncus cerebri bei den Japanern. Arbeiten aus dem anatomischen Institut der Universität Sendai, Heft VI, 1921.

Yamamoto on the basal part of the oblongata. In comparing their illustrations and measurements with those in Swedes, given by Retzius, it seems impossible to state any differences. Microscopically however, G. Fuse [1]) found the medial lemniscus and nucl. funiculi posterioris less developed in the Japanese than in the European.

The brain of the inhabitants of the Dutch Indonesian Archipelago are studied by Sergi [2]), by Kohlbrugge [3]) and by F. A. Kooy [4]), the Philippino's brain by Fallot [5]) and by Ma Wen Chao (l. c. supra).

Of the highly interesting dwarfish Negrito race (which is brachycephalic in contradistinction to the dwarfish African negrillos and the dwarfish Weddahs from Ceylon), and which by Kollmann and several others (e. g. Kleiweg de Zwaan) are considered as very primitive no brains have ever been described.

The Malayan and Javanese inhabitants of the Dutch archipelago are mostly brachycephalic. According to Martin the length width index of the Malays is 82.7, that of the Javanese 84.4.

The average brainweight of the *Malays* is given as 1244 gr.. Sufficiently trustworthy figures for men and women do not exist.

Kohlbrugge studied 36 Javanese brains, 23 of different people of the Malay group (Batak, Bugis, Timorese and Sumatra Malays) and compared them with six Australian brains (those described by Duckworth and Karplus) and ten Dutch brains.

Kohlbrugge's work is very valuable by its exactness of description.

He did not find any racial distinctions either in the ordinary surface pattern, nor after cutting off the surface evenly at a depth of $1/2$ or 1 cm., so that only the more fundamental sulci remain visible.

---

[1]) G. Fuse. Ibidem Heft II Beiträge. zur normalen Anatomie des der spinalen Trigeminuswurzel angehörigen Graus etc. p. 189.

[2]) Sergi. Un cervello di Giavanese. Atti della Soc. Romana di Antrop. Vol. X, 1904.

[3]) Kohlbrugge. Die Gehirnfürchen der Javanen. Eine vergl. Anat. Studie. Verhandeling der Kon. Akad. v. Wetensch. Amsterdam, Sect. 2, Deel XII, 1906; Die Gehirnfürchen malayischer Völker verglichen mit denen der Australier und Europäer, Ibidem, Sect. 2, Deel XV, 1909; Untersuchungen über Grosshirnfürchen der Menschenrassen. Zeitschr. f. Morph. und Anthropologie, 1908.

[4]) F. A. Kooy. Over den Sulcus lunatus by Indonesiers. Dissertation, Amsterdam, published in the Psych. en Neur. Bladen, Amsterdam. 1921.

[5]) Fallot. Le cerveau d'un Malais né à Manille, Bull. Soc. d'Anthrop. Paris 1880.

This method inaugurated by KOHLBRUGGE is rather interesting as some sulci that are deeper in anthropoids (e. g. the intraparietal sulcus), in man may be surpassed in depth by other sulci (e. g. the centralis, CUNNINGHAM), In this respect also racial differences amongst man might occur. So DUCK-WOTH (vide supra) stated that in the Australian the sulc. centralis is less deep than the intraparietal, which thus would be a simian feature (cf. p. 251).

KOHLBRUGGE is also doubtful concerning the character of the lunate sulcus as a remnant of the simian, and cannot accept ZUCKER-KANDL's [1]) opinion (which is also mine [2])) that the lunate sulcus is the bottom fissure of the simian groove. He considers this fissure and the simian bottom sulcus only as „ähnliche" not als homologous fissures (l. c. I. p. 125—126).
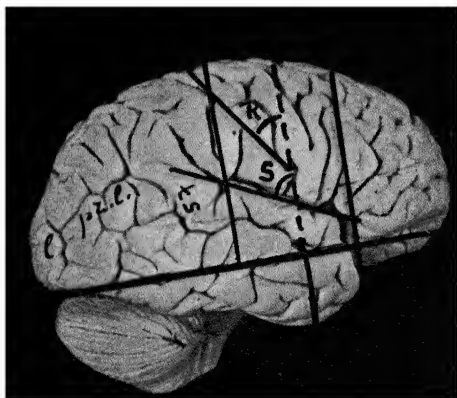
Fig. 143. Javanese brain with exquisite
lunate (*l*) and praelunate (*prl*) sulcus, (continuing
in the superior temporal fissure (t. s.).

The latter standpoint is contested by KOOY as the result of his study of a large part of KOHLBRUGGE's own material, examined in my institute. KOOY demonstrated in about one third of the brains the occurrence of the lunate sulcus in Malayan races, the percentage

[1]) ZUCKERKANDL. Zur Morphologie des Hinterhauptlappens. Arbeiten a. d. neurologischen Institut der Universitat Wien. Bnd. X, 1904, and Zur ver-gleichenden Anatomie der Uebergangswindungen. Ibidem Bnd. 13, 1907.

[2]) ARIËNS KAPPERS. Cerebral localization and the significance of sulci. Report of the XVII internat. Congress of medicine, London, 1913.
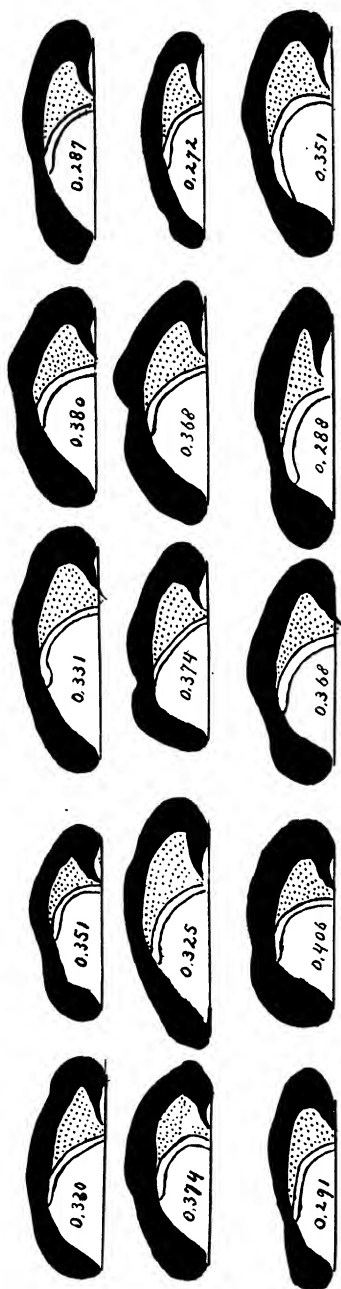
Fig. 144. Fifteen corpora callosa of adult Philippinos. Average callosum height index 0.340; after Ma Wen Chao.

as found in the Dutch. Also the shape of this sulcus is the same in both.

It seems well worthwhile to control the interesting statement of GANS [1]), who found the middle part of the left postcentral convolution, corresponding with the sensibility of the hand, in Europeans nearly always broader than the corresponding part on the right hemisphere, but frequently saw the reverse in Javanese.

The various inhabitants of the Philippine islands are hypsicephalic, excepting the Igorrotes, (KOEZE [2]), and brachycephalic (Baluga's and Negrito's) or mesocephalic (SULLIVAN [3]) and BARROW [4]). Of their brain, however, little is known. It seems to have some mongoloid features.

[1]) GANS. Das Handzentrum in der linken hinteren Zentralwindung. Zeitschr. f. d. gesamte Neur. und Psychiatrie, Bnd. 75, 1922 and Das Handzentrum in der hinteren Zentralwindung bei Javanern Ibidem, Bnd. 85.

[2]) KOEZE. Crania ethnica philippinica. Veröffentlichungen des Niederländischen Reichsmuseums für Völkerkunde, Serie II N°. 3, 1901—1904.

[3]) SULLIVANS researches seem to confirm KOEZE's finding's, at least as far as concerns the length-breadth index (Racial Types in the Philippine islands. Anthropologcial papers of the Amer. Museum of Nat. History, Vol. 23, Part 1, 1918) and so do BARROW's.

[4]) The negrito and allied types in the Philippines. Amer. Anthropologist Vol. 12, 1910. 358.

So MA WEN CHAO (fig. 144) found the callosum index and the septum fornix angles in the Philippinos, though smaller than in the Chinese, larger than in dolichencephalic Dutch. Also the stemangle approaches the Mongol type.

These facts make its desirable to examine the general morphology and fissural brain pattern of these peoples with special reference to the differences observed in the Chinese brain (see pag. 270 and 271).

41—42   22   41 42   22a   22b
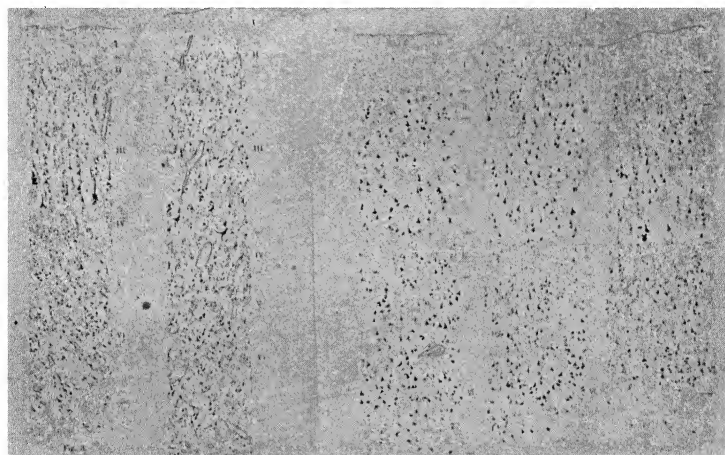
Fig. 145. At the left area 41—42 and area 22 of the temporal region of a normal adult European. At the right, the same areae of a normal adult Madurese. After VAN NOORT.

Cytotectonic researches on the Malayan brain are made by VAN NOORT [1]), who in some cases found the area striata to extend further on the convexity than it usually does in Europeans.

This is the more interesting as BRODMANN found the same in Herero's (cf. p. 265). while ELL. SMITH mentioned it for the Fellahs.

Still the extension of this area is rather subject to variations also in Europeans, and a larger amount of material is necessary for a definite conclusion.

---

[1]) VAN NOORT. The acoustic and visual cortex in the brain of the Madurese. Proc. of the Kon. Akad. v. Wetensch. Amsterdam, 1917.

Another variation, not in the extension, but in the structure of a cortical field is mentioned by VAN NOORT (see fig. 145).

In two male Madurese brains of 36 and 38 years, in which no pathological changes occurred, v. NOORT found the structure of Heschl's gyre very simple, and the acoustic area (41—42 of BROD-MANN) differing from the condition in the European by the total absence of *giant* pyramidal cells in the supra-granular pyramidal layer (III), a thing very rarely observed in Europeans, though the number of these cells shows great variations also here (VERGOUWEN) [1]. Besides the smaller pyramidal cells in this layer were less numerous than in Europeans.

Such a thing seems quite possible since we know from BROD-MANN's [2] fundamental work that the human acoustic area differs very much in structure from the anthropoid area, more so than most other fields and that among the lower mammalian orders it also varies more than most other so called projection areas.

It is desirable that analogous researches be done also in other races on a large and well preserved [3] material so as to obtain average figures.

[1] VERGOUWEN. On the variability of the number of giant pyramidal cells in Heschl's convolution in man. Proceed. of the Kon. Ak. v. Wetensch. Amsterdam, Vol. 19, 1917.

[2] BRODMANN. Vergleichende Lokalizationslehre der Grosshirnrinde in ihren Prinzipien dargestellt. Joh. Ambr. Barth, Leipzig, 1909.

[3] Judging from his figures I am afraid this cannot be said of the material used by STEFKO for his: Beitrag zur Rassenanatomie des Grosshirns: Cyto-architektonik der Regio Rolandica frontalis, area striata und opercularis bei den Chinesen. Zeitschr. f. Anat. und Entwicklung, Bnd. 81, 1926.

Heredity and taxonomic value of brain morphology.

There are several questions directly or indirectly connected with the anthropology of the brain to which I have not, or hardly, alluded.

So a chapter by itself might be written concerning the question as to what is primary skull- or brainform. Though on an average it may be said that the brain determines the form of the skull, there are influences primarily affecting the form of the skull, and consequently that of the brain (see page 214). In those respects, however, where the skull influences the brainform, it should be carefully examined how this influence acts on the brain, not only as far as concerns the general contours but also as far as concerns the mutual arrangement of fissures (see page 211).

Another not less important question is the heredity of brainfeatures. Up to now only little is known about this. Most studies on this subject deal with the morphology of the brain in relatives of the same line, as brothers and sisters (SPITZKA [1]), KARPLUS [2]), WALDEYER [3]), SHUSTER [4]), BOLK [5]), SANO [6])).

As some of this work is done again on twins (identical as well as non-identical twins) those cases should be considered apart from the others.

The latest work on this subject is by SANO [6]) and KARPLUS [7]).

[1]) SPITZKA. Hereditary resemblance in the brains of three brothers. Amer. Anthropologists, Vol. 6, 1904.

[2]) KARPLUS. Ueber Familienähnlichkeiten an den Grosshirnfurchen des Menschen. Arbeiten a. d. neurologischen Institut der Universität Wien, Vol. 12, 1905.

[3]) WALDEYER. Gehirne von Zwillingfruchten Geschlechter. Sitz. ber. der Kön. Preuss. Akad. der Wissensch. Berlin Nr. IV, 1907 and Zeitschr. f. Ethnologie, Vol. 40, 1908.

[4]) SHUSTER. Hereditary resemblance in the fissures of the cerebral hemisphere. MOTT's Archives of Neurology Vol. 6, 1914.

[5]) BOLK. Die Furchen an den Grosshirnen eines Thoracopagen. Folia Neurobiol., Bnd. IV, 1910.

[6]) SANO. The convolutional pattern of the brains of identical twins: a study on hereditary resemblance of furrows of the cerebral hemispheres. Phil. Transact. of the Royal Society London, Series B, Vol. 208, 1916.

SANO. Convolutional pattern of relative brains in man. Proc. of the Royal Society of medicine. Vol. X, 1917, London.

[7]) KARPLUS. Variabilität und Vererbung am Nervensystem des Menschen und einiger Säugetiere. Zweite Auflage, Deuticke, Wien 1921.

The former controlled his results by comparisons with nonrelated brains and found a greater resemblance in relatives, amongst Europeans as well as amongst Negroes.

SANO further found that if the relatives belong to different sexes, the brains are less congruent than among the same sex. KARPLUS' work is interesting on account of his having examined several generations of the same family. Besides KARPLUS did not only study the brain, but also other parts of the nervous system.

In those cases where heredity of fissural pattern was obvious he found that this heredity is equilateral, (not left and right reversed as occurs in identical twins, BOLK). Further he found that sometimes hereditary resemblance only appears on one side. So hereditary factors in brain morphology do certainly occur.

This leads me to consider the taxonomic value of the brain. Is its taxonomic value just as large as that of other parts of the body, e. g. the skull, the teeth, or the extremities, or is it more subject to *individual* variations? This question, which is also of importance for anthropology, has been tested till now chiefly in fishes, by BAUDE-LOT [1]), MAYER [2]), MALME [3]) and most carefully by v. D. HORST [4]). The latter found, on the whole, in the microscopic relations fewer variations in closely related species than in the surface morphology, perhaps on account of the former being more determined by the nervous functions alone, while the latter may be determined by these functions and by additional factors, e. g. the size and form of the skull. This might prove that the intrinsic structure of the brain may have a greater taxonomic and consequently a greater racial value, than its external morphology.

In birds the taxonomic value of the external morphology of the brain has been tested by KÜENZLI [5]).

[1]) BAUDELOT. Étude sur l'anatomie comparée de l'encéphale des poissons, Mém. de la Soc. des Sciences de Strassbourg, Tome VI, 1866.

[2]) MAYER. Ueber den Bau des Gehirns der Fische in Beziehung auf eine darauf gegründete Einteilung dieser Tierklasse. Verhandl. der Kais. Leop. Car. Akad. für Naturforscher, Bnd. XXX, 1864.

[3]) MALME. Studien über das Gehirn der Knochenfische. Kon. Svenska Uet. Akad. Handlingar, Bnd. 17, 1891.

[4]) v. D. HORST. De motorische kernen en banen in de hersenen der visschen hunne taxonomische en neurobiotactische beteekenis, Amsterdam, 1916.

[5]) KÜENZLI. Versuch einer systematischen Morphologie des Gehirns der Vögel. Inaugural Dissertation, Bern, 1918.

This author also found the general morphology of the brain not sufficiently trustworthy for taxonomic studies.

It seems to me that the same result as found by VAN DER HORST appears from fissural and cytotectonic studies of the forebrain in mammals, as there probably is a greater similarity between two individuals of the same sort in the form of BRODMANN's cytotectonic *regions* than in the rather varying pattern of the fissures.

This again agrees with the fact 1 found [1]) that such fissures that have a certain relation to cytotectonic fields (e. g. the centralis and lunate sulcus) adapt themselves only slowly to phylogenetic changes in the form of such fields. These fissures show a distinct retardation in adapting themselves to phylogenetic cytotectonic changes.

So the area striata (17) is gradually pushed backward in phylogeny, but the lunate sulcus bordering it frontally in Prosimiae does not shift pari passu backward with area 17 and consequently in anthropoids and in man it no longer establishes the frontal limit of this area (BRODMANN), but lies in the peri-or parastriate areae (18 or 19). Similarly, the cytotectonic border line of the sensory and motor area in the Chimpanzee already has the same shape as occurs in man, but the total adaption of the central sulcus (especially its lower part) to this cytotectonic border only occurs in man (BRODMANN).

Fissures in a way are more conservative and, consequently, some principal fissures may have a value, for stating *ancestral* relations. So, although in Pithecanthropus, the frontal fissuration, though more developed, in its principal lines strongly reminds us of the Chimpanzee's, it is probable that some of its cytotectonic fields may have been much more developed.

Concluding we see that, the anthropology of the brain is still far behind our anthropological knowledge of other parts of the body.

This is one more reason, however, that we should not lay it aside. If this chapter only has the result that more and better data are gathered, it has not been written in vain.

For this, however, better preserved material is necessary, preferably fixed in the skull by injection of the carotids, or hung in wide pottery by the basil artery thus preventing the brain from touching the container. As soon as it is hardened, the brain should be halved by a medio-sagittal section and the halves further preserved or transported with the mesial surface down.

---

[1]) Cerebral localization and the significance of sulci. Report of the XVIIth international congress of medicine, London 1913.

[2]) For the influence of brain preservatives I refer to HRDLICKA's paper in the Proceedings of the U. S. National Museum, Vol. 30, 1906.

ADDENDA.

It would take a large number of addenda to make this book more or less complete. Giving, however, the structural principles of the nervous system and the main lines of its evolution, I have purposely left out a great many details to keep it as small as possible. Still some addenda from recent contributions may find their place here.

Ad. p. 7. Regarding the phenomena of neurobiotaxis, especially concerning the outgrowth of the neurit opposite the stimulation center I must call attention to a recent publication of PETERFI and KAPEL. Die Wirkung des Anstechens auf das Protoplasma der in Vitro gezüchteten Gewebszellen. Arch. f. experimentelle Zellforschung, Bnd. V, 1928. The authors found that if the neuroblast is wounded it acquires a rounder form and eventually retracts existing offshoots. They further say: ,,Oft, wenn auch nicht immer, löst der Anstich neue Fortsatzbildungen aus, alsob der Stich eine stimulierende Wirkung ausübte.

Die neugebildeten Fortsätze werden auch hier immer an der der Stichstelle entgegengesetzte Richtung angesetzt. Auch dort wo keine neue Fortsätze gebildet werden wächst später derjenige Fortsatz am stärksten der der Stichstelle gegenüber liegt''. This seems to be an analogy of BOK's observation concerning the outgrowth of the axon from the side opposite the stimulation center (p. 11).

In a personal communication Dr. PETERFI writes: Ich bin davon überzeugt dasz Ihre Theorie der Neurobiotaxis nicht blosz eine logisch richtige Hypothese sondern tatsächlich eine Vorhandene und die Entwicklung des Nervensystems bestimmende Erscheinung ist. Ich habe mich ebenfalls mit Dr. KAPEL an die Untersuchung von Neuroblastenkulturen mit Mikroelektroden gemacht und habe gesetzmäszig festgestellt dasz die Axone polar orientiert wachsen und zwar in der Richtung der Anode. This seems to agree with my deductions given on p. 12.

Dr. PETERFI further refers in his letter of Nov. 1928 to a chapter which he is going to write in BETHE's Handbuch, which, as far as I know, has not yet appeared.

Ad p. 16—66. While this book was being printed and the part, dealing with the invertebrate nervous system was from the press, HANSTRÖMS book, Die vergleichende Anatomie des Nervensystems der Wirbellosen, appeared (Jul. Springer, Berlin 1929).

I may not omit to refer those readers who are interested in invertebrate neurology to this standard work, written by a man who has such a great personal experience in this difficult field of our science, and who has given so many important contributions on this subject.

Ad p. 30. Those who are interested in the brainganglion of Polychetes should also consult BINARD and JENNER's contribution to the morphology of the preoral lobe of these animals (Recueil de l'Institut Zoologique Torley-Rousseau, Tome 11, 1928).

Ad. p. 88. In fig. 147, demonstrating the connections of the human parasympathic and sympathic nervous system the gang. jugulare and nodosum vagi are purposely left out as the most recent researches demonstrate the purely sensory character of these ganglia, the g. jugulare innervating the sensibility of the pharynx (MOLHANT), the G. nodosum the sensibility of the heart, lungs, stomach and intestine (MOLHANT), the latter thus being an exquisite sensory visceral ganglion (TERNI).

TERNI also found some sensory cells of the gangl. nodosum to be imbodied in the gang. cervicale supremum (Mon. Zoologico Ital. Anno 36, 1925).

Ad. p. 100, 115. In my short description of the midbrain several ganglia and nuclei had to remain unmentioned. I have not even mentioned the ganglion isthmi, a nucleus lying in the most frontal part of the static area at the level of the trochlear root emergence.

This ganglion already occurs in Selachii (JOHNSTON), and is very large in some Teleosts where it usually lies slightly more frontally in the hind part of the torus semicircularis (see fig. 430 of my Vergleichende Anatomie des Nervensystems der Wirbeltiere und des Menschen, Teil II). It also occurs in Amphibia (ibidem. fig. 444), but acquires its largest size in Reptiles (especially in the Chamaeleon, cf. my Vergleichende Anatomie, fig. 452 and 456). Among Birds, Craigie found it to be very large in the humming bird.

The gang. isthmi consists of at least two parts, the most frontal part may form the medial geniculate ganglion in mammals while some of the largest cells may keep a more caudal position in mammals as nucl. dorsalis lemnisci lateralis or nucleus parabiginimus (Carnivora, Elephas and Man).

Ad. p. 139. A interesting discovery was recently made by Dr. EDW. HORNE CRAIGIE, showing the presence of a small but well laminated area of neocortex in the Kiwi. Apparently in higher birds this primitive condition is dedifferentiated again, their neocortex being represented only in a more diffuse way. CRAIGIE's paper is to appear in the Anat. Anzeiger of 1929. The vascularity of the Kiwi's brain, a valuable addition to the other papers by this author on the bloodsupply of the nervous system in various animals, appeared in the Anat. Record of 1929.

Ad. p. 131 and 141. In his paper: The evolution of the facialis musculature and cutaneous field of the trigeminus in mammals, correlated with the evolution of the central nervous system (of which by the kindness of the author I could read the M. S.). ERNST HUBER studies the comparative anatomical, racial anatomical and embryological relations of the facialis musculature, and cutaneous field of the n. trigeminus and correlates them with the data obtained from neuro-physiological investigations on the cortex.

He comes to following conclusions:

While in lower vertebrates up to the Sauropsida the facialis musculature is but of moderate extension, it has in mammals attained unique development, and the central structures have accordingly evolved.

The motor nucleus of the n. facialis is of corresponding dimensions and has, presumably through neurobiotactic influences, been shifted ventralward. It is subdivided according to the branching of the facial nerve which followed the differentiation of its musculature.

The facialis musculature of the mammals has its representation in the cerebral motor cortex. The motor facial area has frequently been subjected to investigation by many investigators. Although, the available data are very incomplete, in part contradictory, and not at all correlated with the data from studies on the facialis musculature, this much is sure that the motor facialis field is one of the first which in the phylogeny of mammals became definitely localized in the cerebral cortex. Nevertheless in the embryological development of Marsupials and certain Placentals, the facial area becomes responsive to electrical stimuli at a considerably later stage than the forelimb area.

In Monotremes the readily responsive facial area in the motor cortex, however, partly overlaps with the fore limb area. No area for the hind limbs or tail has been detected here.

In Marsupials facial and forelimb areas still overlap to a certain extent. The hind limbs are imperfectly represented, and responses from this area are inconstant.

Within the orders of the Placentals there is a gradual evolution and fuller differentiation of the motor cortex: In Insectivores, Bats, Rodents, and Ungulates the motor cortex appears to have little evolved above the state found in the Marsupials. In the Carnivores (cat and dog) the various motor areas are well defined, and respond with more elaborate movements. Within the Primates finally the motor cortex, including the facial area, attains greatest completeness and highest differention. Stimulation and ablation experiments in monkeys and apes, combined with physiological studies in man and clinical observations in human patients offer an explanation for the well known fact that in central facial palsies the mimic musculature of the upper part of the face is but little impaired.

The vast extension of the motor facialis field is in striking contrast to its limited sensory field, the cutaneous area of which is vestigial.

Together with the superficial facialis musculature, however, the cutaneous field of the n. trigeminus in mammals has attained a high development.

Under the domain of the sensory part of the n. trigeminus is the oral sense (tactile sense of the snout). In close correlation with the olfactory sense the oral sense has highly evolved in mammals. This is reflected in the central nervous mechanism. As to the peripheral structures which serve the oral sense in mammals, the Monotremes have developed along their own line.

The Monotremes through their fundamentally different ground plan of the superficial facial musculature, lack of tactile facial vibrissae and peculiar arrangement of the cutaneous branches of the n. trigeminus, just as in so many other points of their organization, are set aside from the rest of the mammals.

In their ground plan of the superficial facialis musculature, in the possession of a tactile vibrissae apparatus actively moved by facialis muscles and in the arrangement of the facial vibrissae, the Marsupials and Placentals show striking resemblances.

The evolution of the sensory field of the n. trigeminus in Marsupials and Placentals is closely linked up with the acquisition of facial tactile vibrissae. The elaboration of this important head protecting and guiding mechanism was evidently an essential factor in the evolution of the superficial facialis musculature. This in turn goes parallel with the differentiation of the facial area in the motor cortex. In Marsupials and in those Placentals where the facial vibrissae are fully developed, vibrissae movements are an outstanding phenomenon in stimulation experiments on the facial motor cortex. The evolving tactile facial vibrissae apparatus of the common ancestors of Marsupials and Placentals requiring sensory as well as motor representation in higher cortical centers must have played an influential rôle in the early stages of evolution of the neopallium.

The superficial facialis musculature has in the various orders and suborders differentiated to various degrees and along many and very different lines, a fact which makes the superficial facialis musculature of high systematic value. In their ground plan of the superficial facialis musculature, facial tactile vibrissae and distribution of the cutaneous branches of the n. trigeminus, the Prosimians (Lemurs and Tarsius) link up with the other primitive Placentals. Tarsius is specialized and shows unique features in the ear musculature and in the musculature of the eyelids, --- mechanisms which in modern Tarsius have reached a high differentiation with corresponding evolution of the central nervous mechanism.

Further comparative anatomical studies on the superficial facialis musculature in Primates present important data concerning the probable relationship of the lower Platyrrhines to the tarsioid stock and also suggest the possible derivation of the Katarhines from lower platyrrhine forms. They bring further data for the understanding of the genetic relationship of the members of the anthropoid stock, with strong evidence in favor of the view that man must have evolved from the chimpanzee-gorilla stem.

The gradual differentiation of the mimic musculature in the Primates in close correlation with the evolution of the corresponding central structures lead to the elaboration of facial expression, which in man ultimately attained marvellous perfection.

There exist noticeable racial differences in facial expression which are due to structural differences in the mimic musculature, skin and subcutaneous tissue, but more so to differences in psychological reactions.

Experiments proved that muscle sense in the mimic musculature, is conducted together with deep sensibility from the face by the n. facialis, though additional postural sensations may be indirectly appreciated through the sensory trigeminus.

Ad. p. 144. Figure 146, on the next page, taken from the researches by Dr. E. VAN T'HOOG gives a striking demonstration of the relative increase of the supragranular layer in higher mammals.

Ad. p. 150. For a more detailed description of the nervous system of reptiles and birds I refer especially to Dr. E. C. CROSBY's works: CROSBY: The forebrain of Alligator mississippiensis Journ. of Comp. Neurology, Vol. 27, 1917; HUBER and CROSBY. On thalamic and tectal nuclei and fiber-

paths in the brain of the American alligator. Ibidem Vol. 40, 1926, and: The nuclei and fiber paths of the avian diencephalon with consideration of telencephalic and certain mesencephalic centers and connections. Ibidem Vol. 48, 1929 and to Dr. RIOCH's paper: The nuclear configuration of the thalamus, epithalamus and hypothalamus in the dog and cat. Journ. of Comp. Neurology, 1929.
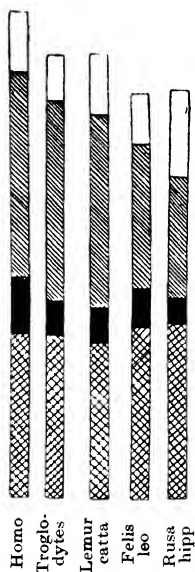
Fig. 146. Relative increase of the supragranular layer in an Ungulate, Carnivore, Lemur, Chimpanzee and in Man. Granular layer black. Supragranular cell layer striped obliquely, subgranular layer crossed. After van t'Hoog.

Ad. p. 221. A very accurate account of fossil brains, mammalian as well ·as lower brains, is contained in the excellent paper: Die Fossilen Gehirne. recently published by Dr. TILLY EDINGER in the Ergebnisse der Anatomie und Entwicklungsgeschichte, Bnd. 28, 1929. This paper, that also contains an extensive list of the literature, should be consulted by everyone who works on this subject.

Ad. p. 234 and 263. I may not omit adding a few words concerning the s. frontalis medius.

This sulcus, though already alluded to by HERVÉ [1]) (1888), was first fully described by EBERSTALLER [2]) (1890) and soon after him amply discussed by CUNNINGHAM [3]) (1892).

---

[1]) La circonvolution de BROCA, Paris, 1888 (no human figures in my abstract) of Tome XI des Comptes rendus de la Societé de biologie.

[2]) Das Stirnhirn 1890.

[3]) Memoirs, No. VII, 1892.

Hervé considered it to be a very important fissure and even gave it a precedence over the other frontal fissures, which according to Cunningham it does not deserve. The former stated that in man it was one of the first, if not the first fissure to appear. Cunningham on the other hand believes that its early appearance is an exception. As a rule Cunningham found the medius to be late in appearance ontogenetically, and considers it as of minor importance. In his Memoirs he gives, however, six instances of such an early development. This certainly would be enough to prove that it is not a sulcus of minor importance. Retzius [1]) also states that it is an important sulcus, appearing to be continuous in 33% of his cases.

The two latter authors state that parts of the fronto-marginal often form its terminal cross piece.

I am inclined to consider the perpendicular branch of Wernicke's fronto-marginal as belonging to the same system as the medius, both probably being related to the rectus of apes (vide infra). Hervé, struck by the early appearance of the frontal half of this sulcus, believes that its breaking up in transverse fissurets in adults is due to a strong development of the region in which it occurs.

The fissure Cunningham describes and figures in adults as midfrontal sulcus certainly is a fissure of minor importance which I met in not even as much as 10% of my brains. In other cases one finds only dimples on the same spot (cf. Cunninghams Memoirs fig. 67).

I am, however, not convinced that this is the same as what Eberstaller and Retzius describe as frontalis medius. Though in shape they resemble each other, as often occurs with neighbouring fissures Eberstaller's and Retzius' sulcus lies somewhat more dorsally and is considerably deeper (1 à 1½ cm.), sometimes even deeper than the frontalis superior. This sulcus resembles more the system figured by Cunningham in a human fetus (fig. 60) where it also tends to connect with what Cunningham calls the horizontal limb (h) on the inferior precentral. This horizontal limb (see also Retzius' fig. VIII) probably corresponds with my fissure 6, being the connection of the midfrontal proper (7) with the precentral (5).

Though this connection mostly fails in recent Europeans, this much is sure that my human 6 and 7 may be easily derived from the 6 and 7 of Pithecanthropus to which fissures in this form no other name than midfrontal could be given. It would then seem that in man this sulcus has acquired a more dorsal position in consequence of a considerable outgrowth of the region immediately above the inferior frontal and moreover may be broken up into pieces, probably by the same cause (see also Hervé).

As 6 and 7 seem to form more often a continuous system in Neanderthal man than in recent men it may be that its being broken up in pieces in most recent brains is indeed a result of further development of the cortex in the foot of the mid frontal convolution, which apparently increases phylogenetically just as much as the inferior frontal convolution. Also the interesting

---

[1]) Das Menschenhirn; Text. p. 105 and fig. VIII.

relation, found by Dr. NAGTEGAAL [1]) in a microcephalic idiot is in favor of this conception, as in this case especially the pallium round the mid frontal sulcus was hypotrophic.

The primitively more continuous character of this sulcus is also found in DUCKWORTH's interpretation (fig. 122) of the Australian aborinigals brain and this may be the reason that in Australians the frontal fissures are more easily demonstrated than in Europeans (p. 251). DUCKWORTH's interpretation agrees with my interpretation in paleolithic casts, though both interpretations were made independently. Underneath fiss. 7 may occur a system of mostly transverse intermediate fissurets, which I do not consider as homologous to EBERSTALLERS midfrontal but that may occasionally fuse to form a system resembling CUNNINGHAMS picture. A peculiarity of the primitive midfrontal is that its frontal part tends to deviate in the direction of, or to fuse with the superior frontal (EBERSTALLER in 44%) thus leaving more space for the perpendicular branch of the fronto-marginal and for intermediate fissurets.

Concerning the phylogenetic origin of the midfrontal sulcus little can be said. In Pithecanthropus it is well pronounced. CUNNINGHAM figures some dimples in front of the superior frontal in the baboon as its simian homologue. I am, however, more inclined to accept that its frontal part (together with the perpendicular branch of WERNICKE's fronto-marginal, with which it often connects) may be related to the rectus of apes, although I know that here I am in conflict with the best connoisseur of fissures, ELL. SMITH [2]). Also KEITH [3]) seems to think so. I have indeed observed in man forms of my fissure 7 that strongly suggest this homology. This would also explain the early development of the frontal part of this fissure and its tendency to lose its continuity in its caudal part that even is less expressed in the simian rectus which is frequently free from the precentral.

This tendency apparently must increase in higher forms as a consequence of cortical proliferations in this area (vide supra).

There is however still a good deal of work to be done on the homology of the frontal fissures and it might be recommended to avoid names and to apply the system I followed in this chapter, using numbers.

---

[1]) NAGTEGAAL. An interesting arrangement of fissures in the brain of a microcephalic idiot. Proceed. of the Kon. Akad. v. Wetensch. Amsterdam, Vol. 32, 1929.

[2]) Catalogue of the Roy. Coll. of Surgeons, p. 475.

[3]) Report on the Galilee skull.

INDEX.

I.

S.

LIST OF AUTHORS.